POPULATION BIOLOGY OF ROSS'S GEESE AT McCONNELL RIVER, NUNAVUT

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By

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GENERAL ABSTRACT

Understanding what influences movement patterns in animals is important to the understanding of colonization, range expansion, and source–sink dynamics. Ross's geese (*Chen rossii*) have been expanding their nesting range eastward, and, as recently as 1994, have been nesting in large numbers in such newly colonized areas. I sampled nests at the McConnell River Migratory Bird Sanctuary (MCR), the largest known Ross's goose nesting colony outside the Queen Maud Gulf Migratory Bird Sanctuary (QMG) to estimate its nesting population size. To understand whether immigration by Ross's geese to a new colony located outside traditional nesting areas has an adaptive basis, I compared nutritional, nesting, and survival metrics between geese nesting at the MCR and those nesting at Karrak Lake (KAR) in QMG. I hypothesized that because of longer nesting season, Ross's geese at MCR would have more fat and protein reserves, larger clutch sizes, and greater nest success than those at KAR. Additionally, I hypothesized that population change at MCR was due largely to *in situ* recruitment. To better understand factors motivating dispersal, movement by Ross's geese between nesting attempts at MCR was measured between years. I hypothesized that dispersal distance of nesting females between years t, and t+1 was a function of both a female's own reproductive success as well as that of her neighbours.

In 1997 over 23,000 Ross's geese were counted at MCR. By 2007, population estimates (± SE) had increased to 81,408 (±12,367). Survival of

both juvenile and adult geese marked at MCR was similar to those nesting at KAR; however, recovery rate estimates were greater than those for KAR. On average, Ross's geese arrived and initiated nests at MCR seven days earlier than at KAR. Abdominal fat was lower when nest initiation date was later in both areas, but was generally greater in geese nesting at MCR. Similarly, there was more indexed protein in geese at MCR than those at KAR in 2 of 3 years. Nesting indices such as clutch size and nest success did not show a consistent area effect, which interacted with a year effect.

Ross's geese at MCR did not appear to use individual or conspecific reproductive success when deciding if or how far to disperse between years, and temporary emigration rates also did not vary based on reproductive success the previous year. Instead, variables other than prior individual or neighbour nest success influenced Ross's goose nest site selection and colony fidelity. The number of Ross's geese nesting at MCR increased at an average rate of 11.4% per year from 2003–2007, despite no increase (0%) from 2006 to 2007. Vital rate information gathered during this time suggests that immigration may have contributed to this growth; however, with few assumptions it can be concluded that MCR is a sustainable population. As a result, studies of geese breeding at MCR provide evidence that arctic geese are capable of successfully colonizing nesting areas great distances beyond historic range.

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CHAPTER 1. GENERAL INTRODUCTION

1.1 BREEDING DISPERSAL

Dispersal is a key parameter in population models, especially in subpopulations where extinction may be avoided through immigration of a small number of individuals (Hanski 1999). The evolution of dispersal can be described in terms of habitat selection: for an individual, the result of moving is the change of their surrounding habitat at a spatial or temporal scale (Clobert et al. 2001). As a result of dispersal, fitness is often influenced by changing habitat quality (Dow and Fredga 1985, Martin 1998), so an understanding of which variables guide dispersal, and therefore habitat selection, will increase knowledge about motivations for temporary and permanent movements.

Theories on the evolution of coloniality are summarized in Siegel-Causey and Kharitonov (1990) and Rolland et al. (1998), and include a spatial hypothesis (shortage of nesting sites), a predation hypothesis, and a food-finding hypothesis (involving information transfer at the colony). Danchin and Wagner (1997) advanced a habitat quality hypothesis, suggesting that the transfer of information at the nesting colony may include cues pertaining to breeding habitat quality.

Colonial nesting occurs in 13% of birds (Lack 1968), and appears to strongly correlate with aquatic habitat, exposure of nests to predators, and a lack of feeding territories (Rolland et al. 1998). Pioneering of new colonies may be motivated in a variety of ways, including searches for high quality

habitat (Doligez et al. 2002, Badyaev et al. 1996) and departure from areas where carrying capacity has been exceeded (Lidicker 1962). Alternatively, colonization of new areas may result from random events such as storms, fire, or human disturbance.

Hypotheses about predation risk based on timing of nest site selection may require a focus on small-scale site selection (within colony site selection), whereas the effects of weather patterns during migration may require a perspective that allows for a focus on large-scale regional movement. Nest site selection may be influenced by random events, energetics, fitness, or any combination thereof. How these variables affect individual movement and breeding decisions may provide insight into large-scale movement. Colony fidelity may have broader implications to species ranges because of resulting changes to migration routes and wintering areas of migratory species. Although movement provides individuals with opportunities to escape deteriorating conditions and improve fitness, dispersal also involves risk (Belichon et al. 1996, Fahrig 2007). Immediate benefits resulting from switches to safer nest sites, areas with more food, or favourable climates may be offset by unforeseen risks such as a different predator community, long-term variability in recruitment, or increased mortality associated with migration to and from new nesting and/or wintering areas.

Animals can be motivated to change breeding locations for many reasons, including resource acquisition (habitat quality), avoidance of

predators or intraspecific competition, facilitation of social interaction, and reproductive performance (Fahrig 2007, Pasinelli et al. 2007). Emigration, whether temporary or permanent, can also be considered in terms of both biotic factors (food availability, predation, disease) and abiotic factors (temperature, sunlight, water availability) (Williams et al. 2002). An estimation of spatial differences in vital rates that relate to components of recruitment (breeding propensity, clutch size, nest success) between traditional sites and those that are newly pioneered can improve understanding of mechanisms that influence dispersal and can be evaluated on both an individual and evolutionary level. However, such comparisons should be accompanied by attention to any differences in nutrition (fat and protein reserves), survival, and movement parameters (immigration, emigration, and breeding propensity) between traditional and new sites because gains in one set of vital rates can be offset by losses in others and may result in either no change or a decline in metapopulation size. As well, identifying forces that drive breeding dispersal on both a small-scale (nest site within the colony) and large-scale (between colonies) should provide more insight into the processes by which dispersal decisions are made.

Major objectives behind management of exploited populations are often to achieve equilibrium between an optimum population and harvest levels. These goals or thresholds are designed to maximize harvest and maintain a sustainable population. Factors such as breeding propensity, clutch size, nest success, movement, and survival influence population size so many of

these factors can be useful in regulating abundance. Additionally, studying these results in a more thorough understanding of population dynamics (Williams et al. 2002). Stable populations can represent sinks where high immigration stabilizes a population with low *in situ* production and survival. Alternately, colony fidelity has potential to become an ecological trap wherein individuals that return to low-quality areas can experience poor reproductive success (Ganter and Cooke 1998). In this case, source colonies can be drained of recruits and over time, population growth is depressed or halted.

1.2 STUDY AREA AND SPECIES

The majority of this study was conducted near the mouth of the McConnell River (60^{o} 50' N, 94^{o} 25' W), 25 km SSW of Arviat, Nunavut, where the river flows into the western side of Hudson Bay. The McConnell River drains a Precambrian sedimentary plain characterized by peat bogs, shallow seasonal streams, and poorly drained shallow tundra ponds (< 1 m) (MacInnes 1962). The sanctuary's northern boundary is 10 km north of McConnell River's northern branch, extending 38 km south along the Hudson Bay coast to the Old Man River (Figure 1.1).

The McConnell River Migratory Bird Sanctuary (MCR) was established in 1960 under the Migratory Birds Convention Act of 1917. The MCR contains nesting habitat for several species of migratory birds including lesser snow geese (*Chen caerulescens caerulescens*), Ross's geese (*C. rossii*), and

small Canada geese (*Branta canadensis parvipes, B. c. hutchinsii*), and was designated as Canada's 14th Ramsar site in 1982. MCR has been a destination for goose research since 1959 when Charles MacInnes began work with small Canada geese (MacInnes 1962). Ross's geese, although occasionally seen since 1959 (MacInnes and Cooch 1963, Prevett and MacInnes 1972), pioneered the northern part of the sanctuary in 1994 (Didiuk et al. 2001). By 1997, over 23,000 Ross's geese were thought to be nesting within a small area north of MCR (Didiuk et al. 2001, Kerbes et al. 2006).

Comparative data were obtained from Ross's geese nesting at Karrak Lake (KAR; 67° 14' N, 100° 15' W) within the Queen Maud Gulf Migratory Bird Sanctuary (QMG) (Figure 1.1). Current Ross's goose research has been active at KAR since 1991, with historic investigation dating back to 1971 (Kerbes et al. 1983).

Ross's geese are small-bodied arctic-nesting white geese. Although similar in appearance to larger lesser snow geese and even larger greater snow geese (*C. c. atlantica*), Ross's geese can be distinguished in the field from both lesser and greater snow geese by their small size, relatively short neck, and unique call (Ryder and Alisauskas 1995). Ross's geese are colonial nesters and nest sympatrically with lesser snow geese at (QMG). However, Ross's goose nest density within MCR is significantly greater than that of the lesser snow goose, but abundance drops sharply in areas where lesser snow geese nest (Didiuk et al. 2001).

Ross's geese use nutrient reserves acquired during migration for both egg formation and to maintain incubation constancy (Ryder 1970, Bon 1996), because few resources are available due to snow cover at the time of arrival. Consequently, distance between habitats where prebreeding food sources are consumed and the breeding destination might affect the proportion of nutrient reserves used for migration, metabolism, and egg production. Additionally, if Ross's geese are breeding in new areas that allow earlier initiation of nests as a result of spring phenology, access to nutrient reserves may be closer geographically and temporally, thereby reducing energy costs associated with usual delays in nesting due to migration distance.

It is thought that more than 90% of all Ross's geese currently continue to nest in the QMG bird sanctuary (Moser 2001, Kerbes et al. 2006). Overall, their nesting population has grown from less than 5,000 in 1931 to currently well over three million (Alisauskas et al. 2008). This growth is also reflected in newer eastern arctic breeding areas where there are likely between 80,000 and 100,000 Ross's geese. Kerbes et al. (2006) accounted for nearly 100 colonies within the QMG metapopulation between 1997 and 1998, and Drake (2006) illustrated the prevalence of movement between these colonies.

1.3 STUDY OBJECTIVES

The main goal of this study is to gain a better understanding of differences between Ross's geese nesting at the (KAR) nesting colony within QMG, and those nesting at the newly pioneered MCR. Differences in population ecology of Ross's geese between these two areas may provide clues to the adaptive motivation for colonization of MCR. Monitoring a new colony and estimating demographic parameters associated with its development further advances understanding of processes by which traditional colonies within the QMG have grown. Drake (2006) demonstrated that probability of movement of Ross's geese between nesting colonies within the QMG metapopulation was common, and showed a general movement from east to west. Similar to lesser kestrels (*Falco naumanni*) (Serrano et al. 2005), Drake (2006) also found probability of movement was greater from small to large colonies than from large to small colonies. Specifically, breeding dispersal probability in Ross's geese was high between certain colonies within the QMG. Considering that MCR is small relative to KAR and Colony 10, the 2 largest colonies in the QMG metapopulation (Kerbes et al. 2006), and is situated in the eastern arctic, I evaluated the likelihood of MCR's persistence as a Ross's goose nesting colony. Growth and persistence of populations depend on recruitment, survival, and immigration/emigration. Based on the location of MCR, Ross's geese that nest there may have different recruitment and survival rates. Recruitment of Ross's geese depends on stored nutrient reserves to overcome nutritional deficits during nesting due to snow cover. Use of

endogenous nutrients allows Ross's geese to initiate nests in the absence of food. As MCR is 800 km farther south than traditional nesting areas in QMG, snowmelt should occur sooner and geese should have more endogenous reserves with which to initiate nests relative to those that nest at QMG; thus, Ross's geese should have more nutrients available for egg development and incubation at MCR than at QMG. A potential greater migration distance for Ross's geese that nest at QMG may also involve greater mortality risk. To evaluate these hypotheses, I compared demographic parameters (nesting vital rates and survival) and dispersal characteristics between this new colony in the low arctic and the traditional and presumable source of colonists from QMG. My specific objectives were to:

1) Compare nutrient reserves of pre-laying females, nest initiation date, clutch size, and nest success of Ross's geese from MCR to those from traditional breeding grounds at KAR. Breeding propensity, clutch size, and nest success may all be affected by the relative amount of nutrient reserves each female can acquire and maintain before initiating nests.
2) Test if breeding propensity and dispersal distance of Ross's geese between years varies according to their nest fate and that of neighbouring females. If colonial nesting in Ross's geese evolved based on public information regarding habitat quality (social constraints hypothesis), then nest site dispersal or breeding propensity could be influenced by conspecific reproductive success.

3) Delineate MCR Ross's goose colony area, estimate nesting population, breeding propensity, adult and juvenile survival, and estimate immigrant contribution to MCR rate of population growth, λ. To evaluate MCR's likelihood for persistence as a Ross's goose nesting colony, vital rates were compared to those from KAR.
4) Test if neckbands reduce survival estimates of MCR Ross's geese and determine whether survival differences are related to active selection by hunters. Objective #2 required the use of neckbands for individual identification of Ross's geese without recapture. When estimating parameters from neckbanded individuals, it is important to understand associated biases. As such, this section tests whether neckbands reduce survival of marked individuals as reported in other studies and, if so, whether this is due to active selection of neckbands by hunters.

Although the reasons for pioneering a new colony in the eastern arctic were unknown, differences in vital rates between this new colony and one of the large colonies at QMG may provide insights into aspects of the population biology responsible for local growth.

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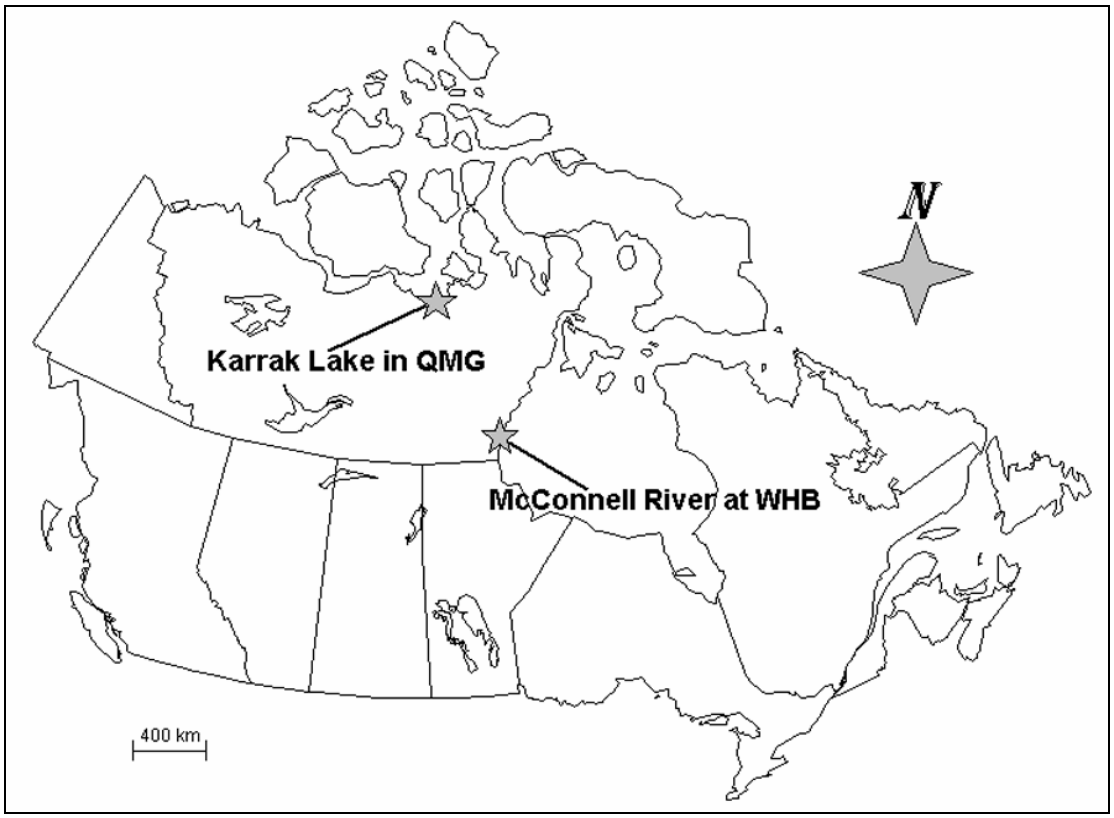

Figure 1.1. Location of McConnell River Migratory Bird Sanctuary and Karrak Lake within the Queen Maud Gulf Migratory Bird Sanctuary.

CHAPTER 2. DO FECUNDITY AND GOSLING PRODUCTION CHANGE WITH LATITUDE IN ROSS'S GEESE?

2.1 ABSTRACT

To test whether benefits have accrued to female Ross's geese (*Chen rossii*) at a recently colonized nesting colony located in the southern arctic, variations in abdominal fat reserves, indexed protein levels, clutch size, and apparent nest success were compared between geese in the McConnell River Migratory Bird Sanctuary (MCR: new, southern colony), and Karrak Lake (KAR: traditional, northern colony) in the Queen Maud Gulf Migratory Bird Sanctuary (QMG). Differences in reserves or vital rates were also compared by year (2003, 2004, and 2005) and as a function of date of nest initiation. Body size was similar in all years between locations. In 2004 and 2005, nests were initiated 24 and 12 days later at MCR than in 2003, but only 12 and 4 days later at KAR in 2004 and 2005 than in 2003. Nest initiation was 13 and 7 days later at KAR than at MCR in 2003 and 2005, but 1 day earlier in 2004. At both areas, abdominal fat deposits were lower when mean nest initiation dates were later. In accordance with nest initiation dates, abdominal fat mass was greater at MCR than at KAR in 2003 and 2005, but similar in 2004. Indexed protein at MCR was similar to rates at KAR in 2003, but greater in 2004 and 2005. Clutch size varied according to a year-by-area interaction, being similar at MCR and KAR in both 2003 and 2004, but greater at MCR in 2005. In 2003 and 2004, apparent nest success was greater at KAR than at MCR, but was similar in 2005. Late snowmelt at

both nesting colonies in 2004 delayed arrival times of geese, initiation of nests, and resulted in depletion of fat reserves. In 2004, nesting was delayed at MCR longer than at KAR, resulting in a more severe decline in all indices of production. Overall, Ross's geese at MCR generally initiated nests earlier with more fat reserves, had marginally larger clutches than at KAR, yet did not realize an overall advantage in nest success. Nutritional advantages of more southerly nesting were overridden by higher but variable predation, suggesting that trade-offs occur when dispersing to new areas.

2.2 INTRODUCTION

The importance of endogenous reserves for reproduction in waterfowl has been discussed at length by many researchers (Ankney and MacInnes 1978, Krapu 1981, Ankney et al. 1991). In particular, Ross's geese (*Chen rossii*) rely on endogenous fat and protein reserves accumulated in spring for egg production (Ryder 1970, Bon 1996) and meeting energetic requirements of incubation (Ryder 1970, Hobson et al. 1993). Stored fat is also the main source of energy for migratory flight (McWilliams and Leafloor 2003). Accordingly, since both lesser snow and Ross's show no increase in fat reserves between spring staging areas on the Canadian prairies and nesting (Bon 1996, Wypkema and Ankney 1979), migration distance should be inversely proportional to endogenous fat catabolized during migration. McConnell River Migratory Bird Sanctuary (hereafter MCR) is ~780 km SSE

of the Karrak Lake colony (hereafter KAR) within the Queen Maud Gulf (QMG) Migratory Bird Sanctuary. Given a potential difference in migration distance and earlier nesting phenology, the energy cost of migration to MCR should be less than for migration to KAR. As long as feeding opportunities and weather conditions along migration corridors to each nesting area are similar, geese that migrate to MCR should have greater fat and (possibly) protein reserves, resulting in a nutritional advantage for these nesting geese compared to those at KAR. I tested this prediction by collecting and subsequently dissecting gravid (hereafter, pre-laying female) Ross's geese upon their arrival at both MCR and KAR colonies. Clutch size and nest success were also compared between sites to estimate fecundity and recruitment, and to assess whether vital rates correlated with the predicted differences in fat or protein reserves. Presumed energetic and nutritional advantages of shorter migration and longer nesting seasons (earlier spring and later freeze at MCR relative to KAR) may explain why Ross's geese pioneered MCR in 1994 and have been increasing in number ever since.

If egg production in Ross’s geese is governed largely by the interplay between endogenous reserves with which they arrive at nesting colonies and phenology of snowmelt (Ryder 1970), then Ross’s geese at MCR should have more fat and/or protein reserves, resulting in larger clutch sizes than those farther north at KAR. As well, incubating females also rely heavily on endogenous fat (Ryder 1970, Hobson et al.1993, Bon 1996). If females nesting at MCR start incubating with more fat, they may exhibit greater nest

constancy, thereby lowering the risk of nest predation (Harvey 1971) and resulting in greater nest success relative to those nesting at KAR.

2.3 METHODS

2.3.1 Study Area

The Ross's geese shot for dissection and all nesting data were collected at nesting colonies within MCR and QMG migratory bird sanctuaries. The MCR colony is located at N 60^{o} 50', W 94^{o} 25' (Figure 2.1). Data from QMG were collected at the Karrak Lake colony of sympatrically nesting Ross's and lesser snow geese, located at N 67^{o} 14', W 100^{o} 15' (Figure 2.1). By 2007, an estimated 80,000 Ross's geese were nesting at MCR within an area of 18.25 km^{2} (Chapter 3). Although Ross's geese have nested there in number since 1994 (Kerbes et al. 2006), the colony had largely been made up of lesser snow geese (*C. caerulescens caerulescens*) beforehand (Kerbes et al. 1990). Kerbes (1994) concluded that 90–95% of Ross's geese nest in colonies within QMG. As at MCR, KAR has expanded and as of 2006 but covers a substantially larger area (215 km^{2}) and contained an estimated 697,000 (± 61,000) nesting Ross's geese (R.T. Alisauskas, unpublished data).

2.3.2 Field Methods

Ross's geese were collected as they arrived at KAR and MCR nesting colonies between mid-May and mid-June. Pre-laying females were identified

and selected for collection after detection of a rounded abdominal profile due to the presence of rapidly developing ovarian follicles or oviducal eggs, and then shot with a shotgun. After verification of sex by cloacal examination (Hochbaum 1942) and age by feather examination (Bellrose 1976), all pre-laying females collected at MCR were then individually bagged, marked, frozen, and shipped to the University of Saskatchewan for dissection. Females were weighed (± 1.0 g) with a digital scale, dial calipers were used to measure tarsus, skull, and keel (± 0.1 mm) (Alisauskas 2002). The body fat for each goose was indexed by mass (± 1 g) of abdominal fat (Thomas et al. 1983), and total body protein was indexed by combined mass of one breast and one leg muscle (Alisauskas 2002).

Clutch size of all nests within 30 m radius incubation plots systematically spaced 500 m apart throughout the colony was recorded during incubation. Average clutch size was used as a metric of breeding effort for comparison between sites. Following hatch, fate of each nest visited during incubation was determined based on the number of hatched egg shell membranes and caps, as well as the presence of gosling down and unhatched eggs. Nests were considered successful if at least one egg hatched.

2.3.3 Statistical Analyses

2.3.3.1 Body Size: Body size can limit the amount of nutrient reserves that can be stored by female geese (Ryder 1970, Ankney and MacInnes 1978), so I first determined whether body size varied among years and study areas

(KAR vs. MCR). The first principle component (PC1) from an analysis (PROC PRINCOMP; SAS Institute 1990) of the correlation matrix of tarsus, skull, and keel were used as a metric of body size (Alisauskas and Ankney 1987); PC1 had loadings of 0.63, 0.52, and, 0.57, respectively, and explained 53% of variation in original measurements.

2.3.3.2 Model Selection and Parameter Estimation: Information theoretic methods were used for model selection (Burnham and Anderson 1998) following a ranking of *a priori* models based on Akaike's Information Criterion, corrected for small sample size (AIC_c). Under this approach, the model with the lowest AIC_c value is considered the most parsimonious model. Separately, I modeled variation in: 1) body size, with models including effects of location (MCR, KAR), year (2003, 2004, 2005), and both an additive and interactive model; 2) abdominal fat; 3) protein; and 4) average clutch size. Abdominal fat, protein, and average clutch size models included effects of location, year, and nest initiation date (continuous), as well as an additive and interactive model with effects of both location and year. All values are presented as least-square means (± 95% CL).

Nest success at MCR and KAR was compared in each year (2003–2005) using chi-square tests (Sokal and Rohlf 1995) in program SAS (PROC FREQ: SAS Institute 1990). Probabilities of nest success were expressed as apparent nest success, i.e., (successful nests / (successful nests + unsuccessful nests)) (± 95% CL). Unsuccessful nests included those that

were destroyed before arrival. This analysis was valid because average probability of nest detection, including previously destroyed nests, was estimated to be 1 during 2003-2005 using Program Distance (Buckland et al. 2001).

2.4 RESULTS

2.4.1 Body Size

From 2003 to 2005, 159 female Ross's geese with developing eggs were sampled upon their arrival to KAR (*N* = 77) and MCR (*N* = 82) nesting colonies. The most parsimonious model explaining variation in body size of Ross's geese was the null model, suggesting little structure to the data. The most saturated model (ΔAIC_c = 6.22), including effects of Area, Year, and an Area-by-Year interaction, accounted for little variation in the data (R^2 = 0.027) (Table 2.1).

2.4.2 Nest Initiation

Mean nest initiation dates were 25 May (MCR) and 9 June (KAR) in 2003, 16 June (MCR) and 15 June (KAR) in 2004, and 4 June (MCR) and 12 June (KAR) in 2005. In 2003 and 2005, nest initiation date (NID) was 13 and 7 days earlier at MCR than at KAR in 2003 and 2005, respectively, but nest initiation dates at the two colonies were similar (±1 day) in 2004 (Figure 2.2).

2.4.3 Nutrient Reserves

The most parsimonious model for variation in body fat included only an effect of nest initiation date (NID) (Table 2.2). Abdominal fat was estimated to decline by 1.6 ± 0.2 grams per day of delayed nesting. In 2003 and 2005, females from MCR initiated nests earlier and with more fat than those at KAR (88.53 ± 6.29 and 69.00 ± 6.20) than those from KAR (76.10 ± 6.43 and 59.90 ± 4.70). In 2004 nests were initiated within 1 day at each location resulting in females collected with similar amounts of fat (50.81 ± 5.61 and 52.11 ± 4.08 at MCR and KAR, respectively) (Figure 2.3).

The best model explaining variation in indexed protein included a year/location interaction (Table 2.3). Protein in females from MCR and KAR was similar in 2003 (184.37 ± 6.62, and 187.87 ± 6.78); however, females from MCR had more protein in 2004 (171.10 ± 5.90) and 2005 (172.27 ± 5.80) than those from KAR (163.33 ± 6.23 and 160.75 ± 5.90). Overall, protein index at both MCR and KAR was greater in 2003 than in 2004 and 2005 (Figure 2.4). Unlike fat, temporal and spatial variations in protein appeared unrelated to lateness of nesting (Table 2.3).

2.4.4 Clutch Size

In total (2003, 2004, and 2005), 3,557 nests were visited at both KAR (*n* = 2872) and MCR (*n* = 1,125). The best model as determined by AIC_c weight ($\omega AIC_c = 0.986$) suggested that clutch size varied by a year-by-location interaction (Table 2.4). In 2003 and 2004, clutch size at MCR (3.38

± 0.09, and 2.97 ± 0.08) was similar to that at KAR (3.45 ± 0.06, and 2.99 ± 0.05, respectively). However, in 2005, clutch size was higher at MCR (2.95 ± 0.08) than at KAR (2.79 ± 0.04). Nevertheless, this model explained only 4.6% of variation in clutch size, suggesting variables not included in competing models may have had a larger impact on clutch size than those modeled. Clutch size was, however, negatively correlated with nest initiation date (r^2 = 0.67, P = 0.047).

2.4.5 Nest Success

The proportion of nests that were successful at MCR (84% ± 2%) and KAR (85% ± 2%) were similar in 2003 (χ^2 = 0.18, n = 1,023, P = 0.6687), but different in 2004 (χ^2 = 16.18, n = 1,199, P < 0.0001) and 2005 (χ^2 = 11.96, n = 1,234, P = 0.0005). In 2004, nest success was greater at KAR (72% ± 3%) than at MCR (58% ± 3%), but greater at MCR (81% ± 2%) than at KAR (71% ± 2% at KAR) in 2005 (Figure 2.6).

2.5 DISCUSSION

2.5.1 Nutrient Reserves

Ross's geese at MCR initiated nesting with more stored nutrients in 2 of 3 years than Ross's geese nesting at KAR. As demonstrated by a negative relationship with NID, which is highly correlated with collection date (R^2 = 0.99), geese had more fat available for egg development and incubation when arrival and nesting was earlier. In 2 of 3 years, nests at MCR were

initiated earlier than at KAR and fat at both locations highly correlated with time of nesting. In 2004, when NID was similar at KAR and MCR, the average daily May temperature in Arviat (30 km north of the nesting colony) was below the lower 95% confidence limit for the 20 year average. In that year, Ross's geese spent 4 weeks staging in Northern Manitoba (250 km south of MCR) awaiting snowmelt further north (R. Rockwell, personal communication). While away from the breeding area, females were presumably utilizing fat deposits at a rate greater than they were able to acquire them for basic metabolism and local movement along the Hudson Bay coast. Delayed nesting at MCR resulted in similar NID (1 day difference) for both nesting colonies and similar amounts of abdominal fat (1.6 gram difference).

MCR geese also had greater indexed protein levels, but protein did not show the same spatio-temporal pattern as fat. After storing fat from a diet that is largely carbohydrate from agricultural seeds on the Canadian Prairies, snow geese switched to green vegetation on the James and Hudson Bay coasts, resulting in storage of protein reserves there (Wypkema and Ankney 1979, Alisauskas and Ankney 1992). Ross's geese also accumulated protein in northern staging areas before reaching the nesting colony at KAR (Bon 1996). Similar to lesser snow geese, Ross's geese thought to be en route to MCR migrate up the Hudson Bay coast, staging at locations including La Perouse Bay, Manitoba. Thus, Ross's geese destined for MCR may have spent more time foraging on protein-rich coastal plants

recently exposed from snowmelt than females migrating to KAR. However, very little is known about the activities of migrating Ross's geese during the period spanning their departure from the Canadian Prairies to their arrival at arctic nesting colonies, particularly for those that migrate inland and west of Hudson Bay such as those that nest at KAR.

Protein reserves were greater in the geese at MCR in two of three years and similar in 2003. When nesting was earliest at MCR in 2003 (14 days before KAR), and the average daily May temperature in Arviat was above the upper (95%) confidence limits for the 20-year average, protein reserves at MCR were similar to those at KAR. Bon (1996) suggested that with sufficient fat reserves for breeding, protein becomes important for determination of clutch size in Ross's geese. The amount of protein estimated to be acquired by staging snow geese on James Bay is approximately equivalent to that found in one snow goose egg (Wypkema and Ankney 1979). Ross's geese that nest at KAR may have less time and possibly less access to relatively high-protein foods such as green vegetation at final staging areas before nesting than those that nest at MCR. Access by MCR Ross's geese to the James Bay and Hudson Bay coast during migration may result in access to richer and more predictable feeding opportunities on staging areas than those that nest at KAR.

In most years, when snowmelt at breeding colonies proceeds on a schedule that permits nest initiation close to the long-term average, associated weather and feeding conditions on final staging areas may have

an important influence on nutrition of Ross's geese that impacts their breeding success. Prolonged migration and delayed nesting due to snowmelt on staging areas and nesting colonies may be favourable to continued protein storage by Ross's geese; however, there appears to be little storage of fat at these staging areas, and prolonged catabolism of body fat without replenishment would result in reduced fat reserves. With staging areas near the nesting colony, female reliance on fat for migration may be less important than supplementing protein reserves for egg production. Thus, there may be an optimum schedule of migration linked to snowmelt, proximity to the nesting colony, and phenology of emergence and growth of the green plants used by Ross's Geese: in early nesting years (2003), there appeared to have been sufficient opportunity to acquire extra protein, and in very late nesting years (2004), fat reserves acquired on the Prairies may have become depleted before arrival at the nesting colonies. This may explain the low fat and average protein levels of MCR Ross's geese in 2004, followed by a year of high fat and average protein in 2005 despite nesting 12 days earlier.

2.5.2 Clutch Size

Clutch size among arctic-nesting snow geese decreases with increasing latitude (Cooch 1961, Dunn and MacInnes 1987). However, in the present study, a difference of 6.5 degrees in latitude between KAR and MCR was not consistently associated with differences in clutch size. Instead, clutch

size negatively correlated with nest initiation date (R^2 = 0.67, *P* = 0.047). Raveling and Lumsden (1977) found a similar trend in Canada geese (*Branta Canadensis*) in the Hudson bay lowlands, and Ryder (1972) found that clutch size in Ross's geese declined by 1 and 2 eggs when the date of the first egg laid was delayed by 2 and 4 days, respectively. In this study, clutch size was greater at MCR in 2005, with protein greater at MCR in 2004 and 2005, with the greatest difference in 2005. Consistent with results presented for Ross's geese at KAR (Bon 1996) and greater snow geese (*C. c. atlanticus*) (Choiniere and Gauthier 1995), protein and clutch size positively correlated with one another (R^2 = 0.66, *P* = 0.050). MCR females had slightly greater protein reserves in 2 of 3 years, and initiated nests on average, 7 days earlier than KAR females. In 5 years of clutch size estimates (Chapter 3), females from MCR had larger clutches in 2 of 5 years and similar clutch sizes in the remaining 3 years. Additional data from Chapter 3 suggests a clutch size advantage at MCR may be realized if the difference in protein and time of nest initiation remains consistent.

2.5.3 Nest Success

Fat reserves are important for maintaining nest constancy (Ankney and MacInnes 1978), and longer and more frequent breaks will increase exposure of eggs to predators and inclement weather, thereby reducing nest success (Harvey 1971, Samelius and Alisauskas 2001). Variables not measured in this study (including weather conditions, and predator

abundance, type, and aggressiveness) likely also affected nest success. Predator communities at KAR and MCR differ considerably. At KAR, the predominant nest predator was the arctic fox (*Alopex lagopus*) with each animal taking 2,000–3,000 eggs per year (Samelius 2006). At MCR, herring gulls (*Larus argentatus*) and parasitic jaegers (*Stercorarius parasiticus*) appeared to be the primary predators of Ross's and lesser snow goose nests. Similarly, MacInnes (1962) saw no arctic fox activity within MCR but described egg predations by jaegers as, "immense". In 2004, females from MCR and KAR had similar but low amounts of fat. In this year, nest success declined relative to 2003 at both locations, but significantly more at MCR (84% to 58%) relative to KAR (85% to 72%). Different predator communities may confound relationships between goose nutrition and nest success. While foxes typically found at KAR take only one egg per visit from nests before caching it away from the nest, avian predators at MCR were frequently observed destroying entire clutches in as little as 5 seconds (J. H. Caswell, personal observation). Since a nest requires only 1 hatched egg to be considered successful, consequences of leaving a nest briefly to compensate for metabolic needs may be more severe at MCR.

Another variable that affected nest success unique to MCR is the egg-collecting activities by residents of Arviat, NU. In years where travel from Arviat is possible, areas of the colony easily accessible from the coast are devoid of nests. The impact of nest removal on overall nest success of the colony is more likely to be noticeable at MCR (14–18.75 km^2) when

compared to a larger colony like KAR (180–200 km^2). Additionally, presence of humans on the nesting colony increases the activity and effectiveness of avian predators. They appear to exploit the disturbance and learn to follow humans while in the nesting colony (MacInnes 1962, J. H. Caswell, personal observation).

In summary, breeding female Ross's geese migrating to MCR initiated nests earlier and consequently with more protein and fat than females migrating to KAR. In 2005, addition to having more protein, females at MCR laid more eggs than those at KAR. Given more time, it may become evident that Ross's geese show fidelity to MCR for nutritional benefits resulting in potentially greater clutch sizes, but are also subject to a different and possibly more aggressive predator community resulting in the similar nest success rates observed. Alternately, variable nest success at MCR may be due to the small size of the colony relative to KAR, and its inability to effectively swamp local predators.

Female survival during nesting was not estimated, but may be different due to the surplus fat available to MCR females retained for incubation compared to KAR females. Despite unstable nest success at MCR compared to KAR, annual survival, breeding propensity, clutch size, and immigration may be sufficient to compensate for years of low reproductive success, resulting in continued growth and expansion of the MCR colony by Ross's geese.

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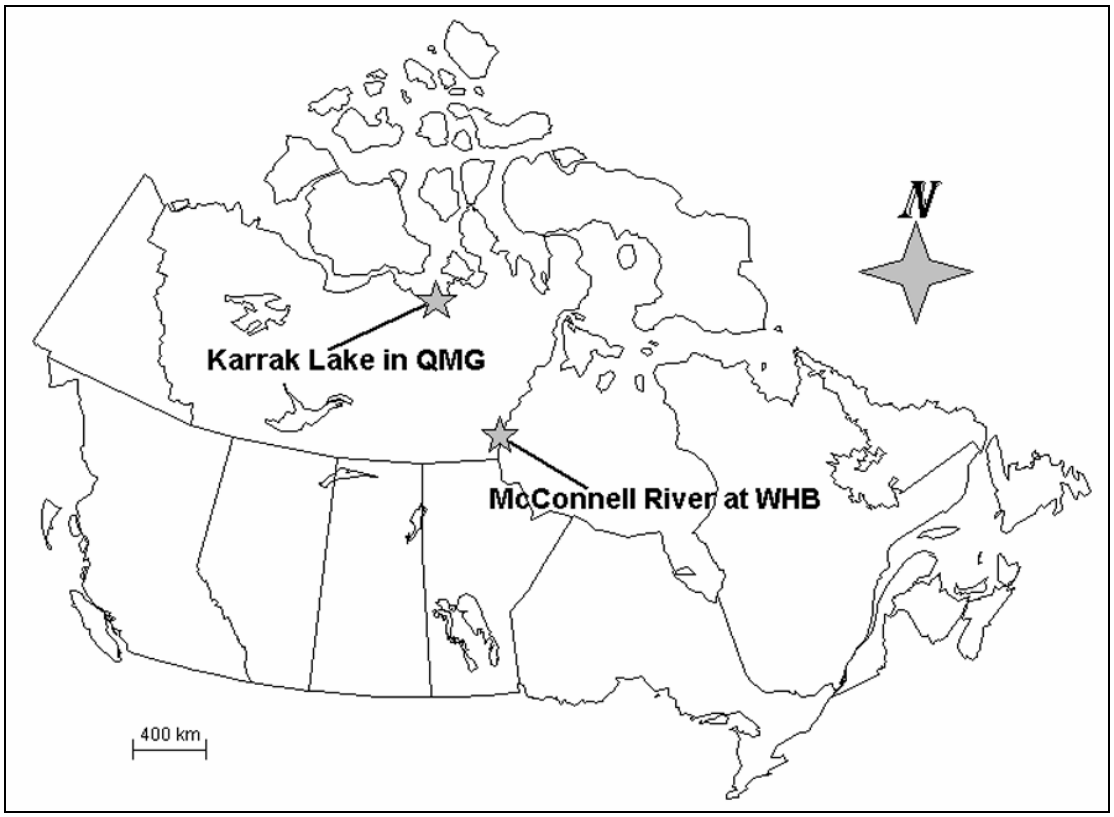

Figure 2.1. Location of McConnell River and Karrak Lake Ross's goose colonies.

Table 2.1. Model structure, number of parameters (*K*), AIC_c, ΔAIC_c, model weight (ω_{AICc}), and the coefficient of determination (R^2) of models used to estimate effects of location (A: MCR vs. KAR) and year (Y: 2003–2005) on body size of Ross's geese collected at McConnell River and Karrak Lake nesting colonies in years 2003, 2004, and 2005.

MODEL	*K*	AICc	Δ	ω_{AICc}	R^2
NULL	2	138.90	0.000	0.403	
A	3	139.15	0.256	0.354	0.011
Y	4	141.26	2.361	0.124	0.011
A, Y, A+Y	5	141.65	2.751	0.102	0.022
A, Y, A*Y	7	145.12	6.222	0.018	0.027

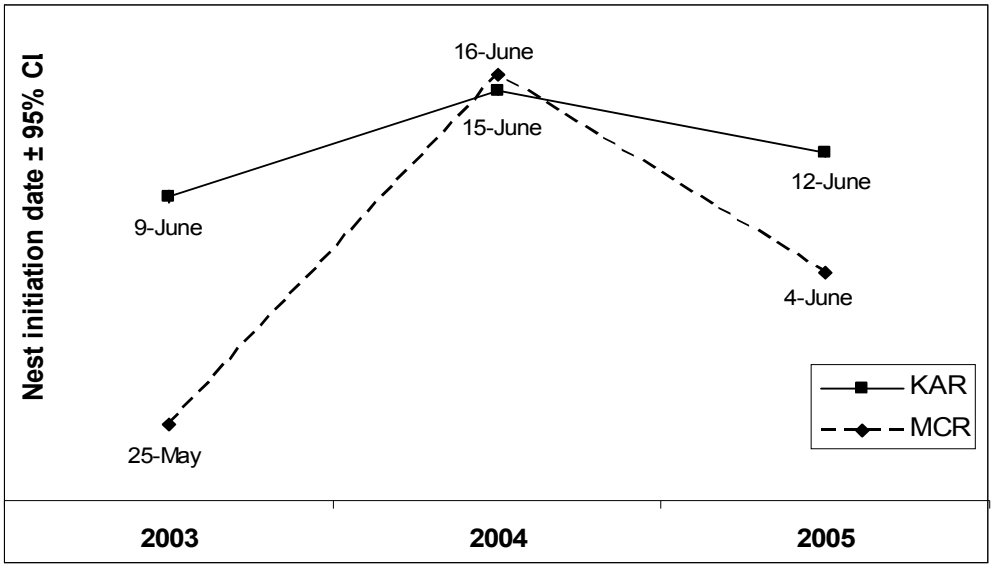

Figure 2.2. Average nest initiation date of Ross's geese nesting at MCR and KAR, 2003–2005 (± 95% CL).

Table 2.2. Model structure, number of parameters (*K*), AIC_c, ΔAIC_c, model weight (ω_{AICc}), and the coefficient of determination (R^2) of models used to estimate effects of location (A: MCR vs. KAR), year (Y: 2003–2005), and nest initiation date (NID: continuous) on the amount of abdominal fat removed from Ross's geese collected at McConnell River and Karrak Lake nesting colonies in 2003, 2004, and 2005.

MODEL	*K*	AICc	Δ	ω_{AICc}	R^2
NID	3	898.61	0.000	0.978	0.357
A, Y, A*Y	7	906.37	7.756	0.020	0.360
A, Y, A+Y	5	911.15	12.538	0.002	0.322
Y	4	917.89	19.273	0.000	0.283
A	3	962.90	64.287	0.000	0.036
NULL	2	966.68	68.068	0.000	

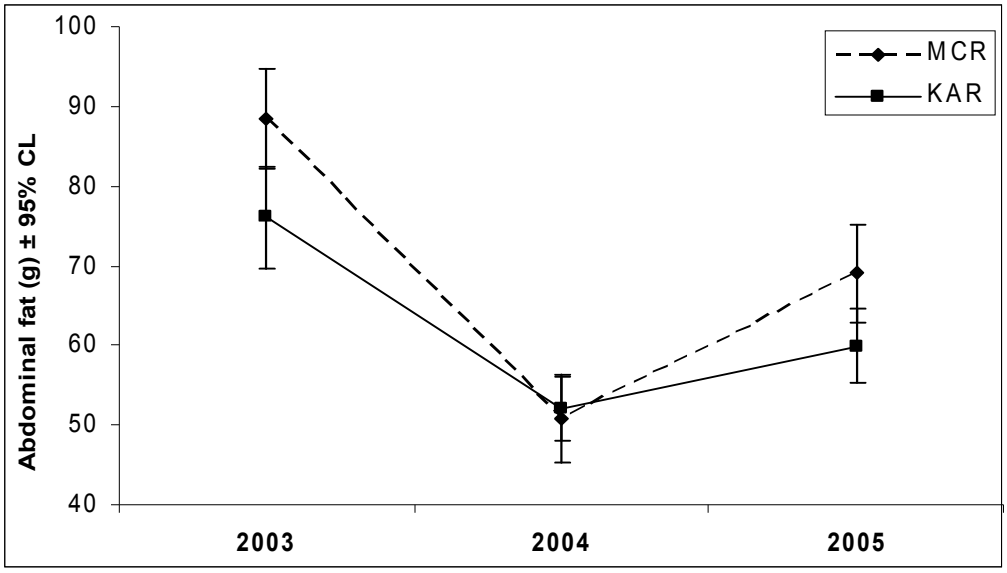

Figure 2.3. Mean abdominal fat (grams) removed from Ross's geese shot at MCR and KAR, 2003–2005 (± 95% CL).

Table 2.3. Model structure, number of parameters (*K*), AIC_c, ΔAIC_c, model weight (ω_{AICc}), and the coefficient of determination (R^2) of models used to estimate effects of location (A: MCR vs. KAR), year (Y: 2003–2005), and nest initiation date (NID: continuous) on the amount of indexed protein removed from Ross's geese collected at McConnell River and Karrak Lake nesting colonies in 2003, 2004, and 2005.

MODEL	*K*	AICc	Δ	ω_{AICc}	R^2
A, Y, A*Y	7	894.63	0.000	0.637	0.267
A, Y, A+Y	5	896.13	1.499	0.301	0.240
Y	4	899.30	4.673	0.062	0.214
NID	3	915.18	20.546	0.000	0.120
A	3	931.49	36.859	0.000	0.025
NULL	2	933.44	38.808	0.000	

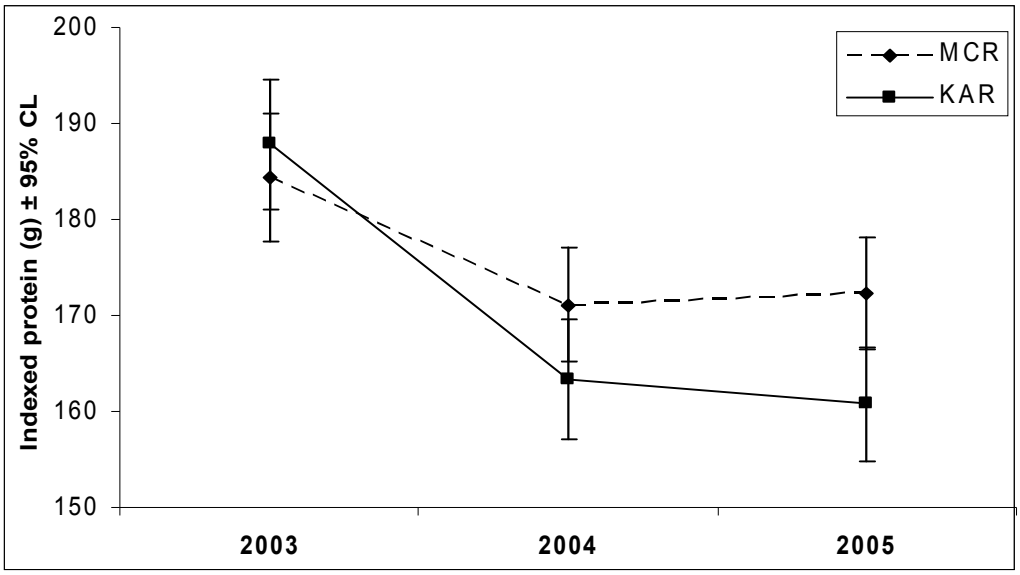

Figure 2.4. Mass of single breast and leg muscle (in grams) removed from Ross's geese shot at McConnell River and Karrak Lake nesting colonies from 2003–2005 (± 95% CL).

Table 2.4. Model structure, number of parameters (*K*), AIC_c, ΔAIC_c, model weight (ω_{AICc}), and the coefficient of determination (R^2) of models used to estimate effects of location (A: MCR vs. KAR), year (Y: 2003–2005), and nest initiation date (NID: continuous) on clutch size of Ross's geese at McConnell River and Karrak Lake nesting colonies in 2003, 2004, and 2005.

MODEL	*K*	AICc	Δ	ω_{AICc}	R^2
A, Y, A*Y	7	-1429.60	0.000	0.986	0.046
Y	4	-1419.93	9.670	0.008	0.042
A, Y, A+Y	5	-1419.41	10.189	0.006	0.042
NID	3	-1372.21	57.387	0.000	0.030
NULL	2	-1251.94	177.665	0.000	
A	3	-1250.85	178.751	0.000	0.000

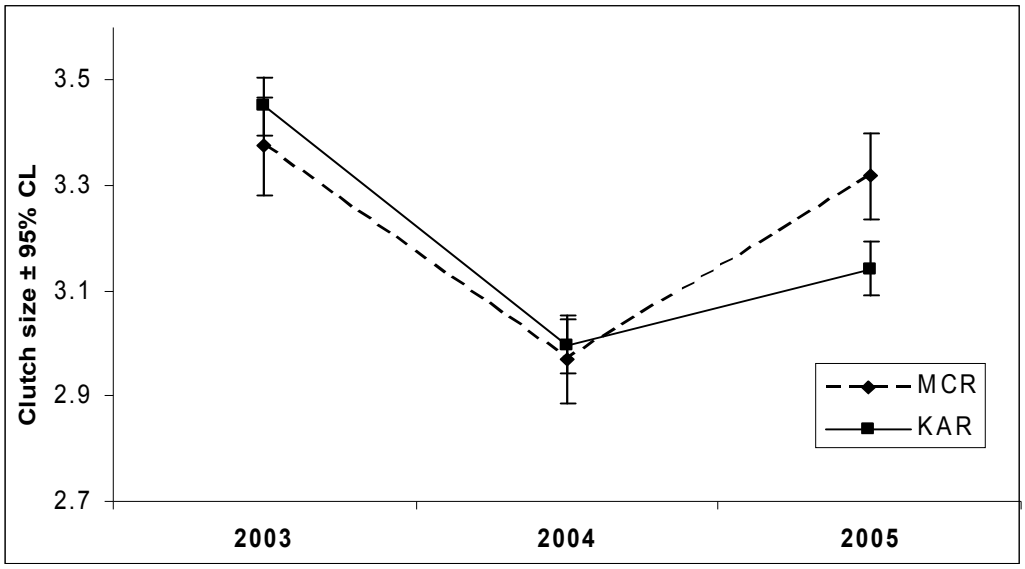

Figure 2.5. Mean clutch size of Ross's goose nests at McConnell River and Karrak Lake nesting colonies, 2003–2005 (± 95% CL).

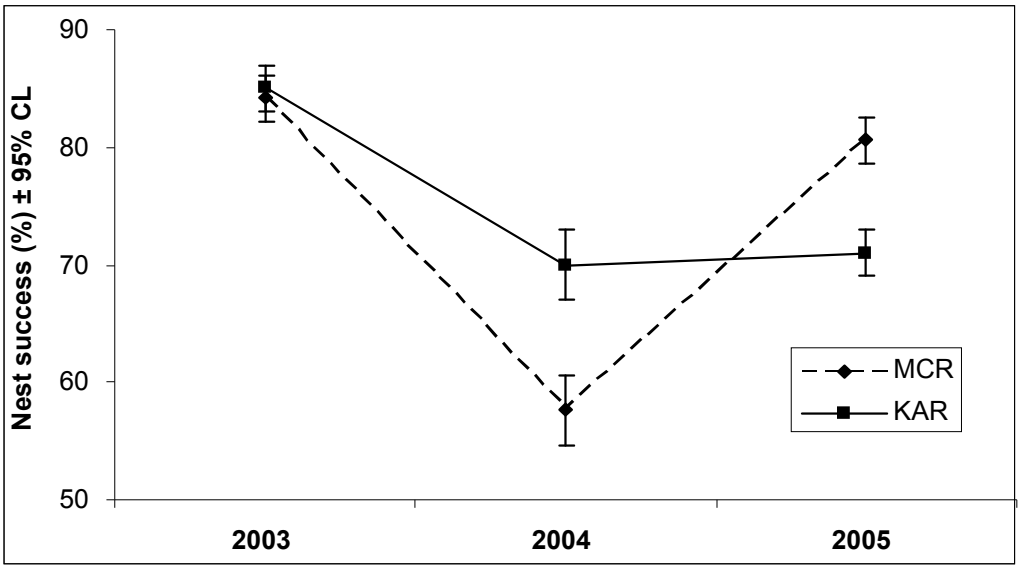

Figure 2.6. Apparent nest success of Ross's geese at McConnell River and Karrak Lake nesting colonies, 2003–2005 (± 95% CL).

CHAPTER 3. A TEST OF THE PUBLIC INFORMATION HYPOTHESIS ON COLONIAL NESTING ROSS'S GEESE

3.1 ABSTRACT

I tested whether Ross's geese (*Chen rossii*) nesting within the McConnell River Migratory Bird Sanctuary (MCR) use individual reproductive success (IRS) and/or reproductive success of neighbouring conspecifics (CRS) when deciding if or how far to disperse the following year. To test the "public information hypothesis" (PIH), I manipulated nest success, applying 1 of 4 treatments to the nest and/or neighbouring nests of marked females (focal females). During 2003, 2004, and 2005, I applied treatments to the nest or surrounding nests of 209, 169, and 239 focal females, respectively. Dispersal response of focal geese was measured where manipulations of nest success were done. Treatment groups were applied to (1) focal geese, (2) their ten nearest neighbours, (3) both focal geese and neighbours, and (4) a control group where nests were visited but no nests were destroyed. Dispersal distance between nesting locations within MCR between years *t* and *t* + 1 did not differ by treatment ($P = 0.82$). Dispersal distance did not vary significantly with reproductive success of focal geese ($P = 0.83$, with focal successful = 1,349 ± 304 m vs. focal unsuccessful = 1,400 ± 298 m) or their nearest neighbours ($P = 0.39$, with neighbour successful = 1,268 ± 332 m vs. neighbour unsuccessful = 1,467 ± 301 m). When modeling temporary emigration, models with 4 treatments ranked last among *a priori* models, and models with grouped treatment effects ranked more poorly than similar

models with those treatment effects removed. Model averaged estimates of temporary emigration were similar for all treatments, as well as when grouped to test for both IRS and CRS. At MCR, cues other than IRS and CRS were more important to Ross's goose decisions about dispersal between 2003 and 2006.

3.2 INTRODUCTION

Some avian species use cues about habitat quality (Clark and Shutler 1999) and breeding performance by conspecifics (Danchin and Wagner 1997) when selecting foraging and breeding areas. Danchin and Wagner (1997) suggested that cues from conspecifics may play a significant role in the evolution of coloniality. In addition to individuals using their own reproductive success (IRS) when deciding if or how far to disperse (Doty and Lee 1974, Gavin and Bollinger 1988, Lindberg and Sedinger 1997), breeding individuals as well as prospectors may consider reproductive success of neighbouring conspecifics (CRS), or "public information," as a cue to predicting average reproductive success the next breeding season (Danchin and Wagner 1997, Danchin et al. 1998, and Doligez et al. 2002). Danchin et al. (1998) demonstrated with black-legged kittiwakes (*Rissa tridactyla*) that the presence of cues such as CRS in year *t* may have attracted individuals to patches of breeding habitat in year *t* + 1.

Until work done by Doligez et al. (2002), support for the public information hypothesis was only correlative and use of CRS solely as a cue

for future dispersal was equivocal. Doligez et al. (2002) manipulated offspring quantity in collared flycatchers (*Ficedula albicollis*) by transferring nestlings between nests. As a result, offspring quality (condition) was reduced in plots where nestlings were added. Doligez et al. (2002) found that emigration rate increased with decreasing offspring quality and quantity. Additionally, immigration by collared flycatchers was greater in plots with greater offspring quantity.

Ross's geese (*Chen rossii*) are an appropriate species with which to test the public information hypothesis because they are colonial nesters and their nesting success or failure is highly visible to their neighbours. After experimental manipulation of nest success, movement of marked individuals within the colony and temporary emigration from the colony during the next breeding season would provide insight into the influence of IRS and CRS on settling behaviour.

I predicted that focal females that nested successfully would have greater nest site fidelity between years relative to those with unsuccessful nests. Additionally, I predicted that unsuccessfully nesting focal females with neighbours that also were unsuccessful would disperse farther during subsequent nesting attempts, and be less likely to attempt to nest at the same nesting colony in year $t + 1$ than those whose neighbours were successful.

3.3 METHODS

3.3.1 Study Area

My test of the public information hypothesis was conducted at a Ross's goose colony within the McConnell River Migratory Bird Sanctuary (MCR) located on the west coast of Hudson Bay, immediately north of the mouth of the McConnell River (60°50' N, 94°25' W), 25 km southwest of Arviat, Nunavut (Figure 3.1). MCR is in the low arctic and contains the largest known Ross's goose breeding colony outside the main breeding concentration in the Queen Maud Gulf Migratory Bird Sanctuary (QMG) (Ryder and Alisauskas 1995, Kerbes et al. 2006).

3.3.2 Field Methods

In early August (2002–2004) at MCR brood rearing areas, flightless molting adult Ross's geese were corralled into nets using a helicopter following methods described by Cooch (1954), and Timm and Bromley (1976). Alternately, all-terrain vehicles (ATVs) were also used to capture geese in 2003 and 2004. While using ATVs, researchers drove along the Hudson Bay coast in search of large, brood-rearing flocks (200–400 adults). When located, two ATVs advanced quickly on either side of the flock and held it in position while a third ATV (with a drive net) searched for a suitably dry banding area nearby. Once the third researcher set up the drive net, geese were guided at walking speed toward the net with two ATVs. Once near the net, all three researchers walked the geese into the net on foot. All geese received a standard USFWS/CWS metal legband. Additionally, a

sample of adult Ross's geese was marked with both metal legbands and plastic neckbands (yellow with black alphanumeric code). In following years (2003–2005), observers used spotting scopes to systematically search MCR during incubation (June) for all neckbanded Ross's geese. When a neckbanded goose was located, neckband code, latitude and longitude, and date was recorded, as well as incubation status (incubating or not). During late stages of incubation, neckbanded females that were found incubating (hereafter referred to as focal females) were sequentially assigned to 1 of 4 treatment groups (trt):

(1) Focal trt: focal female's nest destroyed, with neighbouring nests (10 nearest, or all within a 30 m radius) left unmanipulated.

(2) Neighbour trt: focal female nest unmanipulated while nests of 10 nearest neighbours destroyed.

(3) Focal-Neighbour trt: both focal female and neighbouring nests destroyed.

(4) Control trt: neither focal female, nor neighbouring nests destroyed, with all nests visited.

Following hatch, unmanipulated nests were checked for the presence of egg caps or membranes to indicate if at least one egg had hatched successfully. Nests that had been naturally depredated were reassigned to Focal or Focal-Neighbour treatment (< 10). One year following treatment (t + 1), systematic searches for neckbanded geese and new focal females were also used to relocate focal females from year t.

Movement of focal females within the MCR from year *t* to *t* + 1 was used to measure local dispersal from the nest site (Doligez et al. 2002). Observation of focal females in the nesting colony during incubation (not restricted to those found on nests) in years *t* + 1 indicated a breeding attempt. Those not observed within the colony were assumed to have emigrated and did not attempt to initiate nesting at MCR. Alternately, focal females that failed to breed could have left the colony before they were detected in the sample. Subsequent analyses would not be biased, assuming the treatment applied to focal females the year before did not influence nest success.

3.3.3 Statistical Analysis

3.3.3.1 Dispersal Distance Between Nest Attempts: Nest treatment effects on dispersal distance (meters ± 95% CL) from years *t* to *t* + *1* were modeled and evaluated using AICc model selection procedures (Burnham and Anderson 1998) based on residual sum of squares calculated from analysis of variance (PROC GLM; SAS Institute 2004). A total of 36 *a priori* models were selected for comparison of: all treatments (4 trt; 1 vs. 2 vs. 3 vs. 4); focal female nest success (neigh trt; trt's 1 & 3 vs. 2 & 4); neighbour nest success (neigh trt; trt's 1 & 4 vs. 2 & 3), manipulation (trt vs. control; 1, 2, 3 vs. 4); and a null model (Table 3.2). Distribution of dispersal distance for each treatment was evaluated using box plots and compared using analysis of variance (PROC GLM; SAS Institute 2004).

3.3.3.2 Colony Fidelity: Apparent survival (Φ_i), temporary emigration (γ_i'', γ_i'), as well as capture (p_{ij}) and recapture (c_{ij}) probabilities were modeled using a closed robust design using program MARK (White and Burnham 1999, Kendall 2001). The robust design for sampling marked individuals in this study involved a primary sampling period each year, composed of 2 secondary sampling periods each year, i.e. each year during incubation the nesting colony was searched twice for neckbanded females. To reduce estimated parameters, a Huggins (1989, 1991) estimator was used so that population size was not estimated. All individuals were identified on the colony in year *t*, therefore γ' was set to equal temporary emigration (γ'') since there were no individuals to estimate the probability of non-breeding given that they were not on the colony in year *t*. A cohort-structured model was also used to estimate focal female movement in year *t + 1* during 2003–2006. Models were constructed *a priori* and included both a 2-cohort structure (temporary emigration between 2003 and 2004, between 2004 and 2005, and between 2005 and 2006, with each estimated separately) and no cohort structure. Since observation methods for each secondary sample were systematic and identical, it is improbable that detection probability was Markovian, i.e., that detection of marked individuals in second secondary samples was related to whether they were detected in the first secondary sample. Accordingly, capture probability was set to equal recapture probability ($p_{ij} = c_{ij}$). Additionally, no evaluated model included an effect of

treatment on parameters p_{ij} and c_{ij} as it was assumed that nest fate of marked individuals or fate of neighbouring nests would not influence an observer's ability to detect and read neckbands the following year, assuming the individuals were present at the MCR study area. For both apparent survival and temporary emigration parameters, nest success treatments were modeled similar to nest site dispersal analyses. Quasi-likelihood Akaike's Information Criterion corrected for small sample size and overdispersion ($QAIC_c$) was used to select among all competing models. Model structures within 2 $\Delta QAIC_c$ units of the best model were used to evaluate the importance of each of the selected variables. Parameter estimates were averaged across the entire model set using model weights to account for model uncertainty (Burnham and Anderson 2002) and are presented as maximum likelihood estimates (± 95% CL).

3.3.3.3 Goodness-of-Fit: There are currently no standard goodness-of-fit tests designed specifically for robust design models. Instead, encounter histories were collapsed to mimic a Cormack-Jolly-Seber (CJS) model (Dinsmore et al. 2003). One encounter history was included per year and an individual was considered recovered if it was seen in either first, second, or both secondary occasions. To adjust for overdispersion, I used a variance inflation factor ($\hat{c}$) estimated from median c-hat test (available in Program MARK) of the most parameterized CJS model. Hence, this method of assessing model fit did not account for temporary emigration.

3.4 RESULTS

In total 617 focal female Ross's geese had nests treated in years *t* during 2003, 2004, and 2005, with 258 re-observed within the colony in following years (*t* + *1*). Exact nest locations of 122 focal females were confirmed in years (*t* + *1*) (Table 3.1).

3.4.1 Dispersal Distance Between Nest Attempts

Dispersal distance to subsequent nesting locations between years *t* and *t* + *1* did not differ by treatment ($F_{3, 118}$ = 0.303, *n* = 122, *P* = 0.82) (Figure 3.2). Average dispersal distance (± 95% CL) for all marked females between sequential years was 1,377 ± 437 m, and treatment-specific estimates were 1,262 ± 432 m for focal bird treatment, 1,400 ± 446 m for neighbour treatment, 1,526 ± 414 m when both focal neighbours and neighbours were treated, and 1,277 ± 529 m for control birds. Dispersal distance did not vary by female nest success ($F_{1, 120}$ = 0.048, *n* = 122, *P* = 0.83): successful (treatments #2 and #4 = 1,349 ± 340 m) vs. unsuccessful (treatments #1 and #3 = 1,400 ± 298 m; Figure 3.3). Dispersal distance also did not vary by neighbour nest success ($F_{1, 120}$ = 0.755, *n* = 122, *P* = 0.39): neighbour successful (treatments #1 and #4 = 1,268 ± 332 m) vs. neighbour unsuccessful (treatments #2 and #3 = 1,467 ± 301 m; Figure 3.4).

Results from model selection suggested that the null model was the best approximating model of those considered (Table 3.2). In addition to this null

model, only the neighbour model had ΔAIC_c<2, but it had only about half the support (ωAIC_c = 0.27) compared to the null model (ωAIC_c = 0.52). Models with treatment effects contributed little to the explanation of variation in data and resulted in high model uncertainty.

3.4.2 Colony Fidelity

A total of 36 models were considered, with the most parameterized model including cohort structure and 4 treatment variations in both apparent survival probability (Φ) and temporary emigration (γ") parameters (Table 3.3). Estimated detection probability was $\hat{p}$ = 0.54 ± 0.03 and assumed to be the same among each of the 36 models and is therefore not presented in the results table. Of all models selected for comparison, the null model, {Φ (.) γ (.)}, with no treatment effect and no structure for either apparent survival or temporary emigration parameters, was most parsimonious. Four other competing models were within 2 $\Delta QAIC_c$, suggesting model uncertainty which warranted model-averaging.

Model averaged estimates of apparent survival (Φ) were similar (all confidence limits overlapped) for all 4 nest treatments (Figure 3.5) with little support for variation based on nest success of focal females, neighbouring nests, or an effect of applying a treatment (all models >2 $\Delta QAIC_c$; Table 3.3).

There was some support for treatment effect (i.e. disturbance; trt's 1−3 vs. control; trt 4) ($\Delta QAIC_c$ = 0.56) on temporary emigration of focal females

in year *t + 1*, but there was considerable model uncertainly. Models with 4 treatments ranked last among *a priori* models, and models with grouped treatment effects ranked more poorly than similar models with those treatment effects removed (Table 3.3). Model averaged estimates of temporary emigration (γ ± 95% CL) were similar among all treatments and the control group, and ranged from 0.33 (± 0.11) to 0.37 (± 0.12; Figure 3.6). Support for any treatment effect was small and suggested that temporary emigration rates of females within treatments 1, 2, and 3 was only slightly lower (all confidence limits overlap) than control females (treatment 4; Table 3.3, model {Φ (.) γ (trt vs. control)}, $\omega QAIC_c = 0.10$). Temporary emigration estimates of females with unsuccessful neighbours was slightly lower (all confidence limits overlap) than those with neighbours that nested successfully (Table 3.3, model {Φ (.) γ (neigh trt)}, $\omega QAIC_c = 0.07$).

3.5 DISCUSSION

Many studies have demonstrated that birds with low reproductive success are more likely to disperse than those with higher reproductive success (Gavin and Bollinger 1988, Reed and Oring 1993, Lindberg and Sedinger 1997, Haas 1998, Hoover 2003, Citta and Lindberg 2007). Likewise, successful nest sites are more likely to be occupied in successive years (Dow and Fredga 1985). Reproductive success of conspecific neighbours may also influence dispersal or temporary emigration (Doligez et al. 2002, Pöysä 2006) or selection of nesting patches or colonies (Brown et

al. 2000). Information transfer related to patch quality may be important in the evolution of colonial nesting (Shields et al 1988, Brown et al 1990, Boulinier and Danchin 1997). Although the assumption that a cue for patch quality at MCR was effectively perceived by focal females was not tested, Templeton and Giraldeau (1996) found that public information is exploited more as a cue for patch quality when it is visual (more detectable). I assumed that if focal females were successful when neighbours were not, individuals would perceive their neighbours' absence for the remainder of the nesting cycle. However, when focal-female nests were destroyed, it was uncertain whether they acquired information about the persistence of neighbouring nests. Nests were treated during late incubation, and I observed that nesting females would return as soon as researchers left the immediate area, regardless of whether the focal nests were destroyed. Those with destroyed nests often stood over their nests and may have been distracted from perceiving information about surrounding nests. Doligez et al. (2003) suggested that information transferred about reproductive success likely depends on environmental predictability and interactions between individuals. Nest sites of common goldeneyes (*Bucephala clangula*) in Finland appeared to have high environmental predictability as the probability of nest parasitation was greater if nest sites were successful the previous year. Additionally, females prospected cavities occupied by nesting conspecifics more often than inactive ones (Pöysä 2006), suggesting that interaction with cavity occupants may provide cues for nest safety. Further,

Doligez et al. (2003) found that when habitat quality "varies temporally in a sufficiently predictable way," use of reproductive success by neighbours as a cue for habitat quality the following year may be more advantageous than choosing a site randomly, or basing site choice on philopatry, presence of conspecifics the previous year, or intrinsic patch quality from the previous year. Cadiou et al. (1994) noted that most black-legged kittiwakes prospected during the pre-breeding period to asses patch quality. Conversely, Eadie and Gauthier (1985) found cavity-nesting ducks (*Bucephala spp.*) prospected following hatch or during late incubation. Additionally, Eadie and Gauthier (1985) postulated that prospecting behaviour of ducks was associated with nest-site limitation and delayed maturity. At MCR, nest sites do not appear limited and yearling non-breeders were not seen within the nesting colony following nest initiation. When failed breeders abandoned destroyed nests, they did not appear to spend time in the colony suggesting that little to no prospecting was done by breeding geese. Combined with little evidence of nest site philopatry, these observations suggest Ross's geese at MCR do not use local scale CRS or IRS when choosing subsequent nest locations within MCR, indicating that homogeneous patch quality (Doligez et al. 2003) or additional cues not tested were important when making decisions about changing nest sites between years.

3.5.1 Dispersal Distance Between Nest Attempts

The dispersal distance of Ross's geese in this study did not vary between treatments and was similar when treatments were pooled to examine effects of IRS on dispersal. Dispersal distance of Ross's geese at MCR was less than what was reported by Drake (2006) at KAR, but unsuccessful females at KAR dispersed over 1000 m farther than did successful females. At MCR, females appeared have low nest site fidelity, regardless of IRS or CRS the previous year. As with many arctic-nesting geese (Ankney 1978, Bon 1996), Ross's geese arrive at MCR with developing ovulatory follicles. As these follicles begin to undergo rapid follicular development in the short time before nesting (6-12 days), females may not have time after arrival to nesting areas to wait for specific nest sites to clear of snow. Instead, there may be strong selection for early nest initiation (Slattery and Alisauskas 2002, Drake 2006). Lepage et al. (2000) also found that reproductive success declined with laying date. Similar to scramble competition, Ross's geese compete for nest sites as they became available. Selection for early nest initiation is supported by Ankney's (1978) observations of some female lesser snow geese (*C. caerulescens caerulescens*) arriving at MCR with post-ovulatory follicles, suggesting eggs were dropped before arrival. The energetic cost of egg production may be sufficiently high as to override nest site fidelity in favour of ensuring that developing eggs are not wasted while waiting for an optimal nest site.

3.5.2 Colony Fidelity

Colony fidelity was estimated as the complement to temporary emigration from MCR. Since size of nesting colonies can restrict magnitude of movement and ability to detect differences in movement between treatments, large-scale movement was considered. Models that best explained fidelity in nesting Ross's geese at MCR did not include a treatment effect. Although there was a great deal of model uncertainty, it appears that factors not quantified in this study were more influential in determining whether or not a female Ross's goose temporarily emigrated from MCR. Danchin et al. (1998) noted that emigration of black-legged kittiwakes from nesting cliffs over a period of 17 years was influenced more by CRS than IRS. When evaluating emigration from cliffs, IRS was an important cue on non-productive cliffs, but was often overridden by CRS on successful cliffs. Advantages to site fidelity were described by Lack (1954), Greenwood and Harvey (1982), and Anderson et al. (1992), and stressed the importance of access to, and familiarity with food resources. Ross's geese arrive on nesting grounds when food is unavailable (Gloutney et al. 1999, 2001), however, brood-rearing areas associated with nesting colonies are important to the survival and growth of goslings as well as to the survival and molt of adults. Large-scale fidelity to colonies near high-quality brood-rearing areas may be more important than nest site selection on a smaller scale.

Assumptions for PIH as it relates to nest success of neighboring conspecifics explained in Boulinier et al. (1996) include both patchy and

predictable environments. With kittiwakes, nest success was patchy among cliffs and spatial predictability was based on severity of ectoparasites and predation. Nest success of Ross's geese at MCR varied in response to human egg gatherers who depleted small areas of eggs. The presence of egg gatherers varied annually based on their ability to travel overland, and the specific location of their activities was not predictable from previous years. As a nest predator, egg gathering activity was not predictable, suggesting Ross's geese should have a preference for random nest site selection as described by Doligez et al. (2003). Similar rates of emigration between treatments, and large dispersal distances (relative to colony size) for all treatments, could favour random dispersal strategies, as does the lack of prospecting by non-breeders and failed breeders during incubation and hatch. Avian and mammalian nest predators such as herring gulls (*Larus argentatus*) and arctic foxes (*Alopex lagopus*) nest and breed within and next to the nesting colony, making their activities more predictable between years. However, their foraging movement and intensity may vary. Nests located along the colony periphery may be more vulnerable to predation, suggesting that these locations may be less desirable. Emigration from vulnerable peripheral areas to the centre of nesting colonies via non-random site selection and use of CRS as a cue for patch quality result in nesting at higher densities. This is consistent with anti-predator hypotheses but also results in clustering and high individual fitness cost, supporting the emergence of new colonies (Danchin ad Wagner 1997). Ross's geese

nesting at Karrak Lake support non-random movement as those dispersing between years were more likely to move to areas of higher density than to lower densities (Drake 2006). Although 32.0– 43.5% of the marked birds sighted at an eastern colony within QMG originated from MCR, it is not known if this colony was experiencing net emigration or net immigration. In closely related greater snow geese (*C. c. atlantica*) on Bylot Island Lecomte et al. (2008) found that previous reproductive success had no influence on dispersal distance. Additionally, they were more likely to move from low quality, low density habitat to high quality, high density habitat, regardless of IRS.

This study investigated neighbourhood nest success (successful vs. non-successful), but not quality of success (number of eggs/goslings) and its effect on nest site fidelity. Reed and Oring (1992) determined that the number of prospectors recruited to a population of spotted sandpipers (*Actitis acularia*) was proportional to the number of eggs laid the previous year, not only to the presence of nesting conspecifics or simply a successful hatch. Additionally, manipulative experiments with collared flycatchers revealed that both qualitative and quantitative conspecific reproductive cues were used when making dispersal choices by resident birds (Doligez et al. 2002). Alternately, Citta and Lindberg (2007) found little evidence that breeding dispersal in mountain bluebirds (*Sialia currucoides*) was related to conspecific information. However, dispersal distance was inversely proportional to the number of successful fledglings the previous year.

This is the first study to experimentally test the effect of CRS on the dispersal decisions of colonial-nesting geese. Overall, factors not quantified in this study or random events may be driving nest site selection at MCR. Given the small colony size and low density of nesters at MCR relative to KAR, it is plausible that cues for nest site selection may differ; replicating this study in an area with greater densities and more room to detect dispersal may produce different results. Additionally, using a colony with greater variation in nest success (and perhaps heterogeneous habitat quality) within the colony might produce different results. If so, qualitative attributes such as IRS (Drake 2006) or even CRS, and quantitative attributes such as presence or density of conspecifics might influence nest site selection of this colonial-nesting goose.

3.6 LITERATURE CITED

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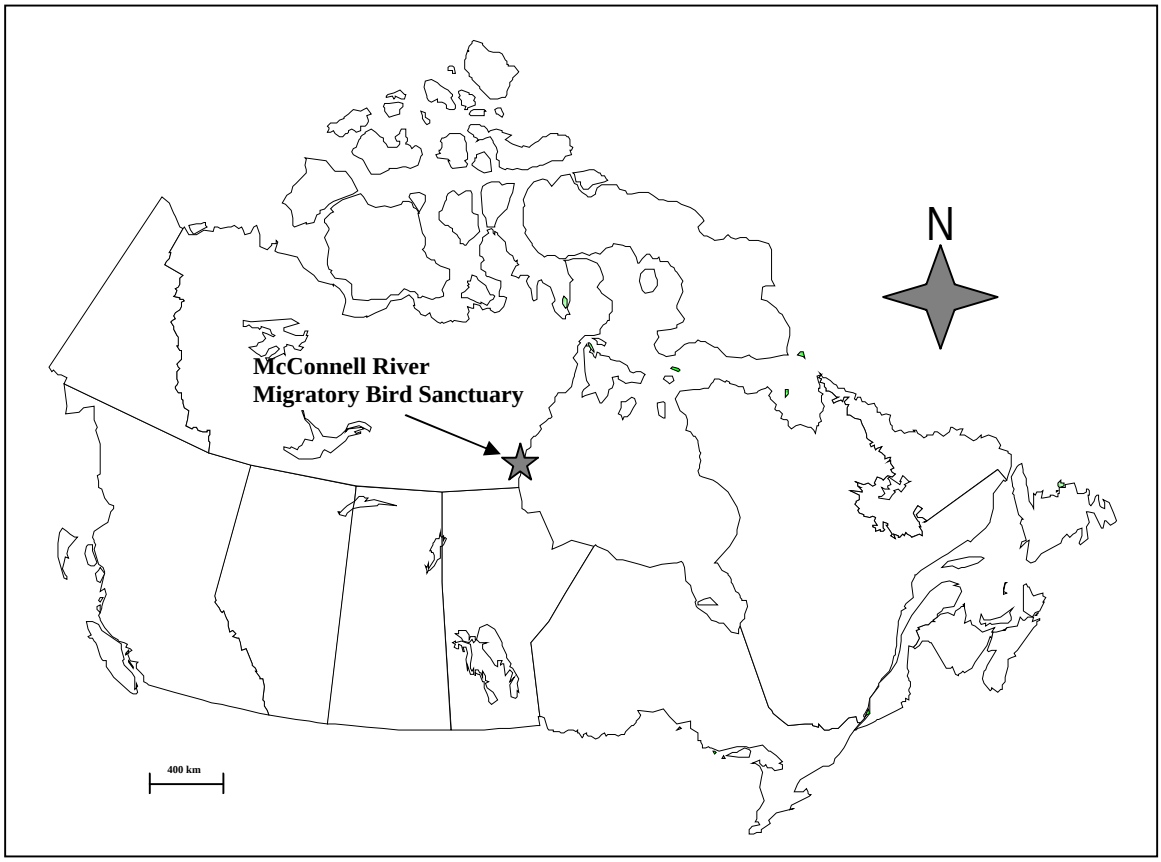

Figure 3.1. Location of McConnell River Migratory Bird Sanctuary, Nunavut.

Table 3.1. Focal female nests found in years *t* (2003–2005) and *t + 1* (2004–2006), and focal females observed in years *t + 1*.

	2003	2004	2005
Treated	209	169	239
Observed t + 1	94 (45%)	62 (37%)	102 (43%)
Nests found t + 1	27 (13%)	49 (29%)	46 (19%)

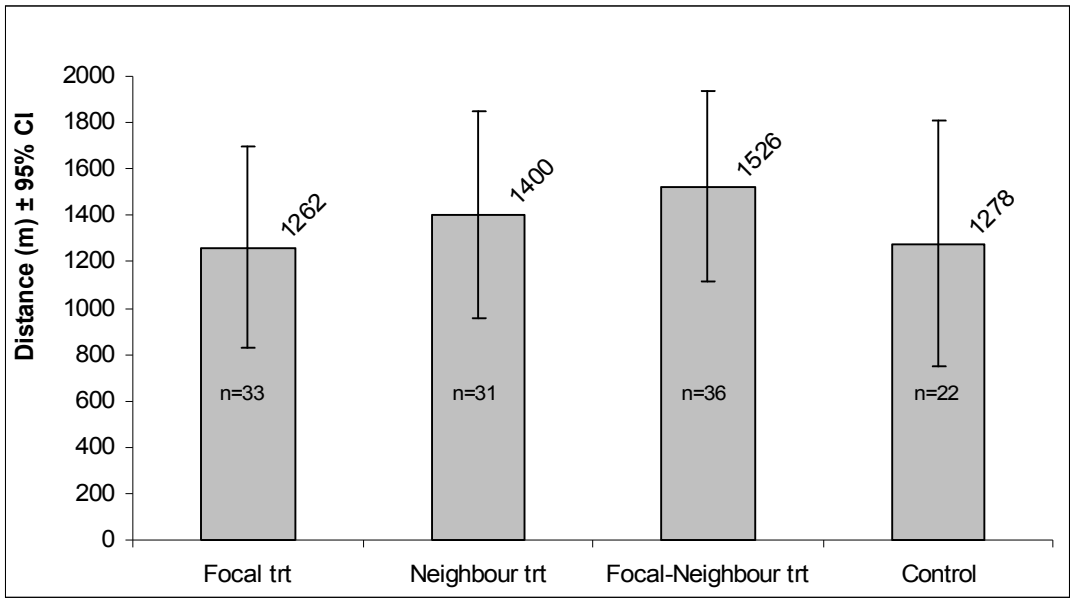

Figure 3.2. Treatment specific dispersal distance (± 95% CL) of focal female Ross's geese between year's *t* and *t + 1* at MCR (2003—2005).

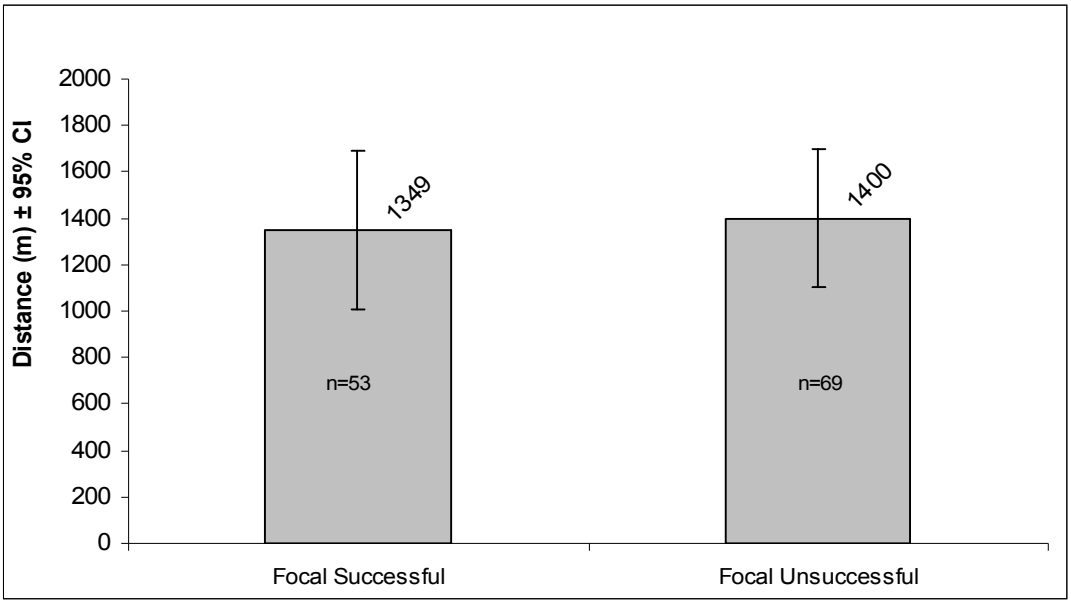

Figure 3.3. Dispersal distance (± 95% CL) of focal female Ross's geese between sequential years from 2003–2006 in response to their nest success at MCR.

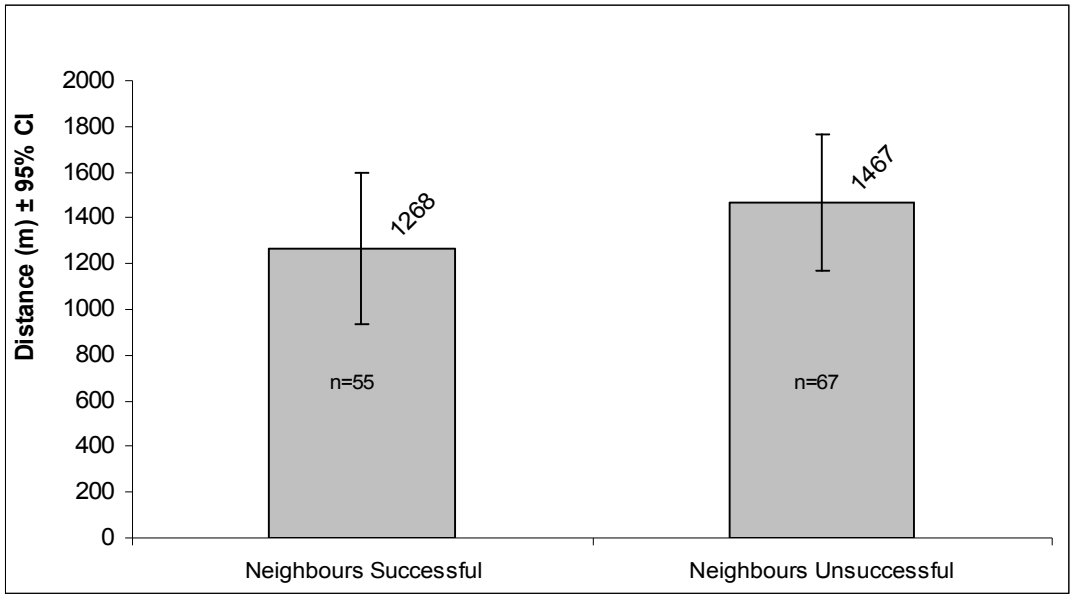

Figure 3.4. Dispersal distance (± 95% CL) of focal Ross's geese between sequential years from 2004–2006 in response to nest success of neighbours at MCR.

Table 3.2. Model structure, AIC_c, ΔAIC_c, model weight (ω_{AICc}), coefficient of determination (R^2) and the number of parameters (K) in models used to estimate effects of treatment on dispersal distance of focal Ross's geese at MCR, 2003–2005.

MODEL		AICc	ΔAICc	ω_{AICc}	R^2	K
Null	(.)	1744.24	0.00	0.43	-	2
Neigh trt	(1+4 vs 2+3)	1745.57	1.34	0.22	0.0063	3
Trt. vs. Control	(1+2+3 vs 4)	1746.17	1.93	0.16	0.0014	3
Focal trt	(1+3 vs 2+4)	1746.29	2.05	0.15	0.0004	3
4 trt	(1vs2vs3vs4)	1749.71	5.48	0.03	0.0077	5

Table 3.3. Model structure, $QAIC_c$, $\Delta QAIC_c$, model weight (ω_{QAICc}), number of parameters (*K*) and deviance of models used to estimate apparent survival (Φ) and temporary emigration (γ) of neckbanded Ross's geese away from MCR in 2004–2006.

MODEL	QAICc	ΔQAICc	ω_{QAICc}	*K*	QDeviance
Φ (.) γ (.)	2616.66	0.00	0.13	3	4141.31
Φ (.) γ (2cohort)	2616.93	0.27	0.11	4	4139.57
Φ (.) γ (trt vs control , 2cohort)	2617.22	0.56	0.10	5	4137.84
Φ (2cohort) γ (.)	2617.75	1.09	0.07	4	4140.39
Φ (.) γ (neigh trt , 2cohort)	2617.97	1.31	0.07	5	4138.60
Φ (.) γ (focal trt , 2cohort)	2618.92	2.26	0.04	5	4139.54
Φ (2cohort) γ (2cohort)	2618.94	2.28	0.04	5	4139.57
Φ (focal trt, 2cohort) γ (.)	2618.99	2.33	0.04	5	4139.62
Φ (2cohort) γ (trt vs control , 2cohort)	2619.23	2.58	0.03	6	4137.84
Φ (trt vs control , 2cohort) γ (.)	2619.25	2.59	0.03	5	4139.87
Φ (focal trt , 2cohort) γ (trt vs control , 2cohort)	2619.40	2.74	0.03	7	4135.98
Φ (neigh trt , 2cohort) γ (.)	2619.64	2.98	0.03	5	4140.27
Φ (4trt , 2cohort) γ (.)	2619.70	3.04	0.03	7	4136.28
Φ (2cohort) γ (neigh trt , 2cohort)	2619.99	3.33	0.02	6	4138.60
Φ (focal trt , 2cohort) γ (2cohort)	2620.18	3.52	0.02	6	4138.78
Φ (trt vs control , 2cohort) γ (2cohort)	2620.45	3.79	0.02	6	4139.05
Φ (neigh trt , 2cohort) γ (2cohort)	2620.83	4.18	0.02	6	4139.44
Φ (.) γ (4trt , 2 cohort)	2620.85	4.19	0.02	7	4137.43
Φ (4trt , 2cohort) γ (2cohort)	2620.93	4.27	0.01	8	4135.48
Φ (2cohort) γ (focal trt , 2cohort)	2620.94	4.28	0.01	6	4139.54
Φ (focal trt , 2cohort) γ (neigh trt , 2cohort)	2621.25	4.59	0.01	7	4137.83
Φ(trt vs control, 2cohort) γ (trt vs control, 2cohort)	2621.26	4.60	0.01	7	4137.84
Φ (trt neigh , 2cohort) γ (trt vs control , 2cohort)	2621.26	4.60	0.01	7	4137.84
Φ (focal trt , 2cohort) γ (focal trt , 2cohort)	2621.61	4.95	0.01	7	4138.19
Φ (4trt , 2cohort) γ (trt vs control , 2cohort)	2621.74	5.08	0.01	9	4134.26
Φ (trt vs control , 2cohort) γ (neigh trt , 2cohort)	2621.81	5.15	0.01	7	4138.39
Φ (neigh trt , 2cohort) γ (neigh trt , 2cohort)	2621.97	5.31	0.01	7	4138.55
Φ (4trt , 2cohort) γ (neigh trt , 2cohort)	2622.05	5.39	0.01	9	4134.58
Φ (4trt , 2cohort) γ (focal trt , 2cohort)	2622.33	5.67	0.01	9	4134.86
Φ (trt vs control , 2cohort) γ (focal trt , 2cohort)	2622.47	5.81	0.01	7	4139.05
Φ (neigh trt , 2cohort) γ (focal trt , 2cohort)	2622.83	6.17	0.01	7	4139.41
Φ (2 cohort) γ (4trt , 2 cohort)	2622.88	6.22	0.01	8	4137.43
Φ (focal trt , 2 cohort) γ (4trt , 2 cohort)	2623.46	6.80	0.00	9	4135.98
Φ (neigh trt , 2 cohort) γ (4trt , 2 cohort)	2624.88	8.22	0.00	9	4137.40
Φ (trt vs control , 2 cohort) γ (4trt , 2 cohort)	2624.91	8.25	0.00	9	4137.43
Φ (4trt , 2 cohort) γ (4trt , 2 cohort)	2625.10	8.44	0.00	11	4133.56

* Capture (*p*) and re-capture (*c*) parameters are not presented above, but are assumed equal and set constant in all models; see text.

**Emigration (γ) represents both γ" and γ' since all individuals were identified on the colony before movement was estimated.

***2cohort models only consider movement in year *t*+1, (.) models pool all years

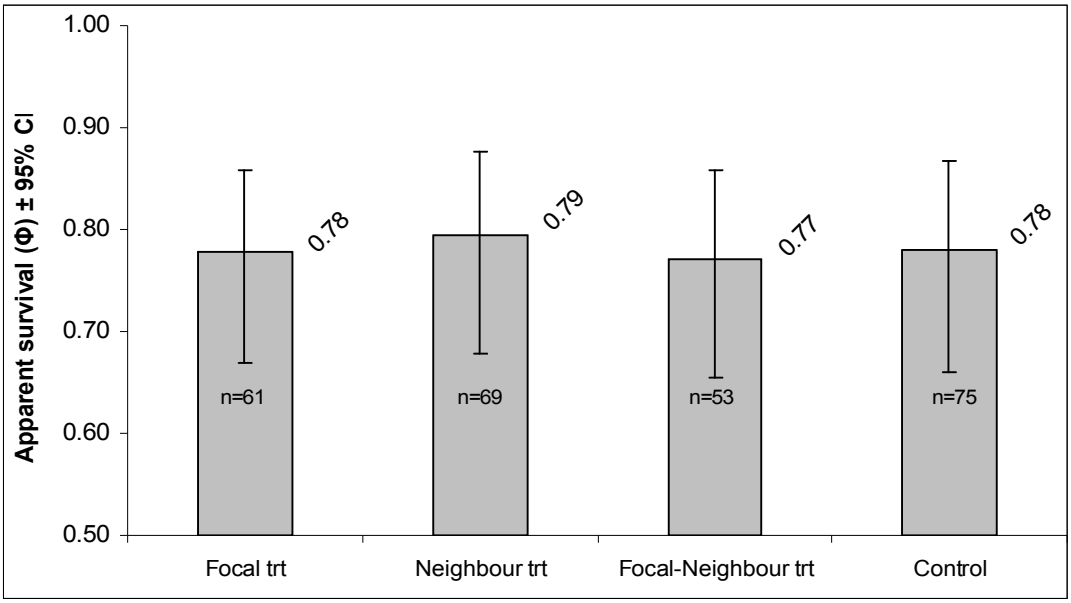

Figure 3.5. Model averaged estimate of apparent survival (Φ ± 95% CL) of focal females at MCR between year *t* and *t + 1*, by treatment (2004–2006).

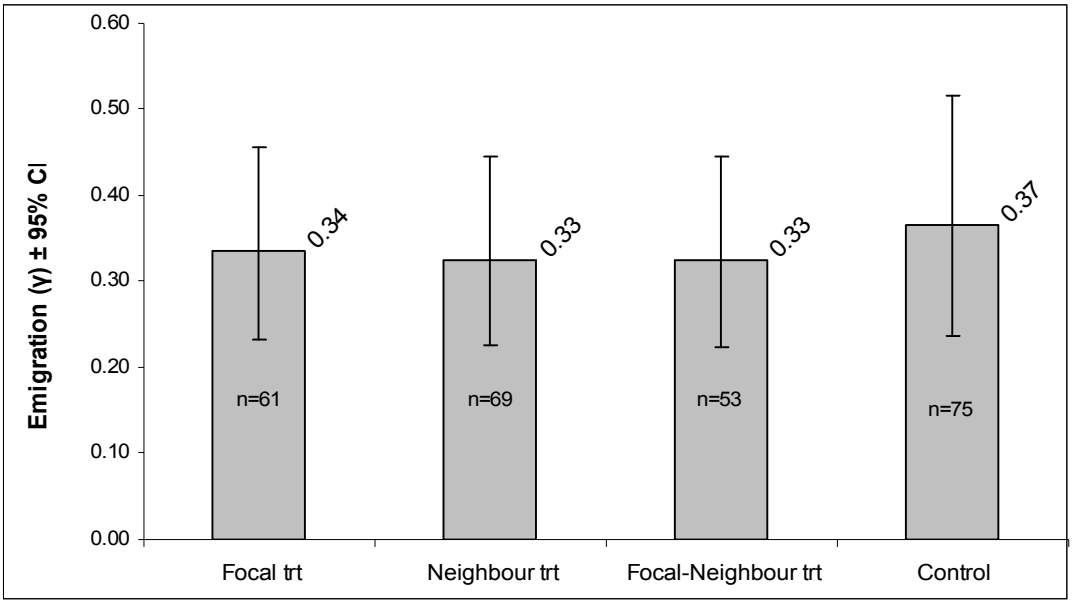

Figure 3.6. Model averaged estimates of temporary emigration (γ ± 95% CL) of focal females at MCR in year *t* + *1*, by treatment (2004–2006).

CHAPTER 4. DEMOGRAPHY OF ROSS'S GEESE AT THE McCONNELL RIVER COLONY

4.1 ABSTRACT

Concurrent with their population explosion, Ross's geese (*Chen rossii*) have expanded their breeding range to areas where, as recently as 1994, there was little evidence of a breeding population. By 1997, the McConnell River Migratory Bird Sanctuary (MCR) was thought to contain over 23,000 Ross's geese. As of 2007, estimates of over 80,000 Ross's geese suggest that growth of the MCR population was as rapid as traditional colonies within the Queen Maud Gulf Migratory Bird Sanctuary (QMG). I estimated vital rates, breeding propensity, as well as survival and recovery rates for a recently established nesting population of Ross's geese at MCR, and compared them to those available from Karrak Lake (KAR), an older established colony farther north. This was done to determine the population size trajectory at MCR and determine the relative contribution of various vital rates to population growth rate. Ross's geese nesting at MCR initiated nests on average 7 days earlier than those nesting at KAR. Clutch size and nest success were similar between locations, as were annual survival estimates of both adult and juvenile geese marked on nearby brood-rearing areas. However, recovery rate estimates for both adult and juvenile Ross's geese nesting at MCR were greater than those for KAR. Ross's geese are firmly established in Canada's eastern arctic, and the nesting populations are growing at a rate similar to that at KAR.

4.2 INTRODUCTION

Light goose population growth has resulted in localized habitat degradation and destruction in migration stopover, nesting, and brood-rearing areas (Batt 1997). Ross's geese (*Chen rossii*) are colonial-nesting geese, with 95% of the known continental breeding population nesting within the Queen Maud Gulf Migratory Bird Sanctuary (QMG) (Kerbes 1994, Kerbes et al. 2006). Since discovery of their arctic nesting grounds in 1940, the North American Ross's goose population increased from 2,000−3,000 in the early 1950s to over 1 million by 2001 (Alisauskas and Rockwell 2001). Concurrent with an increase in population size, Ross's geese have shown an eastward shift in spring and fall migration routes (Dzubin 1965), wintering range (Ryder and Alisauskas 1995), and nesting areas (Cooch 1954, Kerbes et al. 2006). Before this eastward shift, Ross's geese were harvested predominantly in California and Alberta, and were not recorded in Central, Mississippi, and Atlantic flyways until 1974, 1982, and 1996, respectively (Moser and Duncan 2001). Although Pacific flyway harvest of Ross's geese increased from the 1960s to 1990s, the proportion of U.S. harvest in the flyway declined from 100% to 29%; simultaneously, the Central and Mississippi Flyway proportions increased from 0% to 56%, and from 0% to 15%, respectively (Moser and Duncan 2001).

In 1994, Inuit hunters near the McConnell River Migratory Bird Sanctuary (MCR) (Figure 4.1) reported Ross's geese in their spring harvest, which previously included only snow geese. By 1997, 23,400 nesting Ross's geese

were counted in an area representing 1.4% of the MCR light goose colony (Didiuk et al. 2001, Kerbes et al. 2006). The annual growth rate of the nesting colony at Karrak Lake (KAR), the largest colony within the QMG, was estimated to be 9.7% annually from 1993 to 2000 (Alisauskas and Rockwell 2001). Assuming a similar growth rate, the nesting population of Ross's geese at MCR was predicted to have been ~40,800 at the onset of this study in 2003.

To better understand population dynamics of MCR Ross's geese, my objective was to estimate several components of recruitment and juvenile and adult survival in an attempt to determine whether the colony at MCR was sustainable through *in situ* production, or whether its persistence was largely a result of dispersal from larger colonies in the central arctic. Nests sampled in plots within the colony were used to estimate the population size of nesting Ross's geese from 2003–2007, from which a rate of population growth, $\lambda = N_{t+1} / N_t$, was estimated. Survival was estimated from individually-marked birds that were recovered by hunters (Brownie et al. 1985).

Ross's geese have been marked with legbands at MCR since 2002, permitting estimation of survival and recovery probabilities. KAR and other nearby colonies in the central arctic may be source populations for eastern arctic Ross's geese, but little is known about their movement to MCR since there have been no detailed studies at MCR since Ross's geese first colonized the area in 1994. I collected information about the number of

nesting Ross's geese, average clutch size, nest success, juvenile and adult survival, and breeding propensity to provide insight into which vital rates might be driving population growth of Ross's geese nesting at MCR.

The broad objective of this work was to compare demographic parameters and overall population growth rates of a new Ross's goose colony at MCR and a traditional colony at QMG. Specific objectives were to: delineate the MCR Ross's goose colony area; estimate nesting population size as well as juvenile and adult survival rates; and to estimate the potential contribution of immigrants to the annual rate of population change, λ, at MCR. Considering MCR was a large lesser snow goose colony as recent as the mid-1980's (Kerbes et al. 2006) it is likely that sufficient resources for a sustainable Ross's goose colony exists. Since habitat degradation has been hypothesized for the significant decline in lesser snow goose nesting activity at MCR (Kerbes 1990, 2006), it is questionable that it could now support a growing population of Ross's geese without sufficient regeneration of vegetation.

4.3 METHODS

4.3.1 Study Area

Nesting studies were done within the MCR colony, (60^{o} 50' N, 94^{o} 25' W), 25 km south of Arviat, Nunavut (Figure 4.1). This colony is located in the low arctic (Polunin 1951, Walker 2000) and is the largest known colony of nesting Ross's geese outside of QMG (Kerbes et al. 2006). Mass capture of

geese for marking with legbands occurred on coastal brood-rearing areas immediately east, north, and south of MCR. Nesting studies were also done concurrently at KAR (67° 14' N, 100° 15' W). Central arctic banding drives occurred along the QMG coast northwest, north, and northeast of KAR.

4.3.2 Field Methods

For nesting analyses, Ross's goose nests were distinguished from lesser snow goose (*C. caerulescens caerulescens*) nests using discriminant function analysis of egg lengths and widths, averaged for each clutch (Alisauskas et al. 1998); this method accurately classified 100% of 61 known Ross's and 100% of 64 known lesser snow goose nests from MCR in 2003 (J. H. Caswell, unpublished data). Known Ross's goose nests were identified as those with at least one parent (incubating eggs, picking at nest, or showing nest defense) having been previously neckbanded as a Ross's goose. This shows that one of the parents has been identified as a Ross's goose in the hand at a prior date. Known lesser snow goose nests were identified by the presence of at least one blue phase adult. As Blue phase Ross's geese are exceedingly rare, and dissimilar to blue phase snow geese, the presence of a blue adult in addition to typical morphometric cues (body size, culmen characteristics, plumage) minimized the risk of mis-identification.

4.3.2.1 Population Size: Sample units for estimation of population size were 30 m radius plots spaced 500 m apart throughout the nesting colony (Alisauskas et al. 1998, Buckland et al. 2001). All nests (both active and destroyed) found within plots were counted. A tape measure (50 m) was affixed or held at the centre of each nesting plot (marked with an orange-flagged stake) while a researcher walked in concentric circles throughout and measured the distance of each nest from the centre of the plot (for estimation of nest detection probability within the plot, Buckland et al. 2001). Each nest was marked with a uniquely identifiable 5" wooden stake < 2' from the nest. A compass bearing to each nest from the center of the plot was recorded to facilitate revisiting the nests to determine fate. The location of each plot was recorded on a hand-held Global Positioning System (GPS) using the Universal Transverse Mercator (UTM) grid.

4.3.2.2 Colony Delineation: The perimeter of the MCR Ross's goose nesting colony was determined by presence of ≥1 Ross's goose nest within 250 m of plot stakes. Nesting plots were placed every 500 m until no Ross's goose nests were detected within 250 m. Plots spaced systematically every 500 m resulted in the equivalent of 4 complete plots per km^2. The colony area was calculated by dividing the number of plots that had a minimum of 1 Ross's goose nest within 250 m by 4 (plots per km^2).

4.3.2.3 Components of Recruitment: Eggs were marked with both nest and egg number from oldest (egg 1) to youngest with a permanent marker. The oldest egg in each nest, identified by degree of staining (Cooper 1978), was aged by floating it in an adjacent wetland (Westerskov 1950, Walter and Rusch 1997). The nest age was backdated to estimate nest initiation date, assuming an incubation period of 22 days. Clutch size was also recorded during nest counts, but did not account for egg attrition during laying. To quantify nest success, all nests marked during incubation were revisited following hatch. Nest bowls were searched for evidence of a successful hatch, indicated by presence of egg membranes or egg caps. A nest was judged to be successful if there was evidence of at least one hatched egg.

4.3.2.4 Survival: The annual survival of Ross's geese at both MCR and KAR was estimated using band recoveries from birds shot by hunters (Brownie et al. 1985). From 2002–2006, flocks of breeding adult Ross's geese with young were marked with metal legbands in mass banding drives along the MCR and KAR brood-rearing areas using all terrain vehicles (at MCR only) or helicopters (Timm and Bromley 1976). Ross's geese at both MCR and KAR were marked with both neckbands and legbands; however, survival analyses were restricted to those with only legbands to avoid biased survival estimates from neckbanded individuals (Alisauskas and Lindberg 2002, Alisauskas et al. 2006). A sample of geese was marked with neckbands to allow for repeated observation on the nesting colony within and between

years to gather immigration and emigration rates. Recovery data for birds marked during this period were obtained from the Bird Banding Laboratory in Laurel, Maryland.

4.3.2.5 Breeding Propensity: From 2003–2006, observers walked a systematic grid throughout the MCR colony twice during incubation, reading neckbands with spotting scopes. As neckbands were only applied to breeding adults (adults with goslings) and no obvious non-breeding geese were seen within the nesting colony during the incubation period, all neckbanded geese detected at the colony were assumed to have attempted nesting at MCR that year. Given this, breeding propensity is the inverse of temporary emigration and any goose who did not attempt to breed was considered to have temporarily emigrated from the MCR nesting colony.

4.3.3 Statistical Analyses

4.3.3.1 Population Size: Program Distance (Thomas et al. 1998) was used to estimate nest density and nest detection rate within circular plots at MCR. After reviewing detection probability histograms for evidence of systematic errors (e.g., loading of nests at particular distances), data were grouped at 10 m intervals (Buckland et at. 2001) to improve model fit and maximize detection, especially near 0 m. A 2-step modeling process was used to select the best model. First, to best fit the density function, data were modeled with three key functions (uniform, half normal, and negative

exponential). The uniform key function best fit the shape of the density function based on evaluation of histograms. This was appropriate considering detection was consistent through the entire plot (Buckland et al. 2001). Second, I attempted to improve model fit by adding series expansions (cosine, simple polynomial, and hermite polynomial). In these cases, adding series expansions did not improve model fit, so only a uniform key function was used (Buckland et al. 2001). AIC_c based selection criteria were used to rank competing models while data fit was assessed by selecting for low coefficients of variation, narrow confidence limits, and goodness-of-fit of $\chi^2 \geq 0.05$. Due to high model uncertainty (all 3 models <2 ΔAIC_c) and biases associated with selecting only one model, annual nest density estimates were model-averaged across all competing models using calculated Akaike weights, w (Burnham and Anderson 2002, Wunder et al. 2003). Annual estimates (± 95% CL) of nest density (nests per km^2) were then multiplied by colony area (km^2) to provide an estimate of the number of nests within the colony, and then by 2 to provide an estimate of breeding adults (*N*). Annual MCR population growth (λ) at each interval was estimated as follows:

$$\lambda = N^{t+1} / N^{t}$$

4.3.3.2 Components of Recruitment: Average nest initiation date, clutch size, and nest success were calculated using program JMP 5.1.2 (SAS Institute 1989). Estimates of nest success are presented as apparent nest

success (± 95% CL), since nest detection estimates within plots averaged 0.90 for 2003–2007 and egg gathering by residents of nearby Arviat, Nunavut, during laying and early incubation resulted in non-constant nest survival over time, violating an assumption of Mayfield's (1961) method for estimation of nest success. From 2003–2007 nest detection estimates ranged from 0.74 (2007) to 1.0 (2003–2005).

4.3.3.3 Survival: Brownie et al. (1985) models in program MARK (White and Burnham 1999) were used to estimate both annual survival ($\hat{S}_i$) and annual recovery ($\hat{f}_i$) probabilities of legbanded Ross's geese from MCR and KAR. Models were constructed *a priori* and included: time dependent and constant survival and recovery rates, age effect, an effect of banding location, and a time trend. Data were pooled by sex as annual survival does not appear to vary appreciably between sexes in Ross's geese (Melinchuk and Ryder 1980). Goodness-of-fit of the global model $\{S_{(c*a*t)}\ f_{(c*a*t)}\}$ was tested using 100 parametric bootstrap simulations with program MARK. The global model included 36 estimable parameters where 'c' represents colony (KAR vs. MCR), 'a' represents age (HY vs. AHY), 't' represents year, and 'T' represents a time trend. Deviance from data was greater than 95% of the simulated deviances suggesting a lack of model fit. A variance inflation factor ($\hat{c}$ = 1.4973) was therefore used to adjust variance estimates. Akaike's Information Criterion adjusted for small samples size and overdispersion ($QAIC_c$) was used to rank models from the candidate set.

Models within 2 $\Delta QAIC_c$ units of the best model were used to evaluate importance of each of the selected variables relative to one another. Parameter estimates were averaged across the entire model set using model weights to account for model uncertainty (Burnham and Anderson 2002), and are presented as maximum likelihood estimates (± 95% CL).

4.3.3.4 Breeding Propensity: Robust design models (Kendall 2001) in program MARK were used to estimate apparent survival (Φ_{ij}), temporary random emigration (γ_{ij}), and capture and recapture ($p_{ij,}$ c_{ij}) probabilities of neckbanded adult Ross's geese between 2003 and 2006. To reduce estimated parameters, a Huggins (1989, 1991) estimator was used so that population size was not estimated. Survival was assumed to be constant based on concurrent Brownie et al. (1985) estimates from a larger legbanded sample of adult Ross's geese at MCR. Models with both constant and annual variation in temporary emigration and capture probability were evaluated. Since observation methods for each secondary sample were systematic and identical, it is unlikely that detection probability of marked individuals at MCR was different between the first and second secondary samples. Accordingly, capture probability was set to equal recapture probability ($p_{ij} = c_{ij}$). Quasi-likelihood Akaike's Information Criterion, corrected for small sample size and overdispersion ($QAIC_c$), was used to rank quality of competing models. Parameter estimates were averaged across the entire model set using model weights to account for model

uncertainty (Burnham and Anderson 2002) and are presented as maximum likelihood estimates (± 95% CL).

There are currently no standard goodness-of-fit tests designed specifically for robust design models. Instead, encounter histories were collapsed and fit to a Cormack-Jolly-Seber (CJS) model (Dinsmore et al. 2003): an individual was considered to have been encountered in a year if it was seen in either first, second, or both secondary occasions. To adjust for overdispersion or poor model fit, a median c-hat test was done on the most parameterized model, after which sampling variance from robust design models were inflated by c-hat estimated in the CJS model. Observed deviance was greater than 95% of the simulated deviances, suggesting a lack of model fit. Variance inflation factor ($\hat{c}$ = 5.3457) was estimated to adjust variance estimates. Akaike's Information Criterion (AIC) adjusted for small samples size (AIC_c) and overdispersion ($QAIC_c$), was used to select among all competing models. This method of assessing model fit did not account for temporary emigration.

4.4 RESULTS

4.4.1 Population Size

Model averaged parameter estimates of nest densities (nests per km^2) ranged from 1,824 (*CL* = 1,356–2,455) in 2004 to 2,680 (*CL* = 1,853–3,875) in 2003 (Table 4.1). Model averaged estimates for probability of nest detection ranged from 0.74 (*CL* = 0.60–0.92) in 2007 to 1.00 (*CL* = 1.00–

1.001) in 2003–2005 (Table 4.1). MCR Ross's goose nesting population estimates increased steadily from 2003 (53,592) to 2006 (82,852) and then stabilized in 2007 (81,408) (Figure 4.2). Annual estimates of population growth rate (λ) for nesting Ross's geese at MCR during corresponding intervals were 7.2%, 20.1%, 18.8%, and –0.5%, with average λ for the period (2003–2007) estimated to have been 11.4%.

4.4.2 Components of Recruitment

The colony size of Ross's geese at MCR increased between 2003 and 2006 (14.00–18.75 km^2), then decreased slightly in 2007 (18.25 km^2) (Table 4.1). Over the same period, mean nest initiation date (NID) varied annually by up to 23 days (2003 = 25 May, 2004 = 16 June). NID at KAR varied by a maximum of 10 days (2006 = 8 June, 2007 = 18 June) and was later than MCR in all years except 2004 (1 day earlier) (Figure 4.3). Average NID between 2003 and 2007 was 1 week earlier at MCR (5 June) than at KAR (12 June). Apparent clutch size (MEAN ± 95% CL) at MCR (3.19 ± 0.09) was similar to that at KAR (3.15 ± 0.05). Annually, clutch sizes were similar in 3 of 5 years; however, in years when they were different (2005 and 2007), clutch size was greater at MCR (Figure 4.4). Average apparent nest success between 2003 and 2005 was similar at MCR (74.3 ± 2.3%) and KAR (75.3 ± 2.0%). Annually, nest success was similar at MCR and KAR in 2003 (84 ± 2.0% vs. 85 ± 2.0%, respectively), greater at KAR in 2004 (70 ± 2.9% vs. 58 ± 2.9%), and greater at MCR in 2005 (81 ± 2.0% vs. 71 ± 2.0%) (Figure 4.5).

4.4.3 Survival

Between 2002 and 2006, 20,812 adult and 13,947 gosling Ross's geese were marked at MCR and KAR brood-rearing areas. Hunters harvested, retrieved, and reported 744 geese marked as adults and 700 geese marked as goslings, respectively, by the end of the 2006-2007 hunting season. The best model suggested that survival varied only by age of geese, while annual recovery rate varied by age, colony, and year (Table 4.2). Model averaged estimates (± 95% CL) of annual survival for adult Ross's geese (0.83 ± 0.07) were greater than for juveniles (0.38 ± 0.10) in all years. Survival estimates were similar in all years and at both locations (MCR vs. KAR) (Figure 4.6). Overall, recovery probability (± 95% CL) varied from 0.013 (± 0.002) to 0.059 (± 0.013). Estimates declined from 2003–2006, were greater for juveniles than for adults, and greater for geese marked at MCR than at KAR (Figure 4.7).

4.4.4 Breeding Propensity

Of the 4 models considered, the best was the most parameterized and included constant survival and temporal variation in both temporary emigration and capture probability parameters (Table 4.3). This model was 26.2 times better supported by the data than the next best model. Model averaged parameter estimates suggested that breeding propensity (1-γ) was lowest in 2004 (0.50, *CL* = 0.32–0.67), and greater in both 2005 (0.75, *CL* =

0.51–0.90) and 2006 (0.80, *CL* = 0.47–0.94) (Table 4.4). Capture probability (detection) was similar from 2003–2005, then declined in 2006 (Table 4.4).

4.5 DISCUSSION

4.5.1 Population Size

Colonization and subsequent population growth of nesting Ross's geese at MCR followed a decline in nesting lesser snow geese from a peak of 230,000 in 1985 to 65,500 in 1997 (Kerbes et al. 2006). Kerbes et al. (1990, 2006) suggested that lesser snow geese had degraded coastal salt marsh habitat along the west coast of Hudson Bay to the point where their nesting range had to be expanded from as low as 160 km^2 to 759 km^2, thereby resulting in lower nest densities in recent years. During this study (2003–2007), nesting Ross's goose estimates were restricted to 17–22 km^2 (i.e., the known Ross's goose nesting area). Although it appears Ross's geese occupy a region that was once favoured by both lesser snow (Kerbes et al. 1990) and Canada geese (Lieff 1973), it is not currently known if the overall snow goose population within the larger MCR area has declined from a level similar to that of 1997. Canada geese, however, utilize a similar area as historically indicated while sharing it with recently established Ross's geese (Baldwin 2006). From 2003–2007, population change at MCR was similar to that at KAR, 11.4%, and 11.9% (Alisauskas, unpublished data), respectively. Kerbes (1994) estimated that numbers of Ross's geese at QMG doubled from 1965 to 1976 (34,000 to 77,300), then more than doubled again by

1988 (188,000). By 1994, when ~10,000 Ross's geese were discovered to be nesting at MCR (Didiuk et al. 2001), there were an estimated 190,000 Ross's geese nesting at KAR (Alisauskas, unpublished data). From 1997 (first nesting population estimate) to 2003, the MCR population had increased by 223%, a rate similar to that at KAR (235%) during the same interval (methods used to generate the 1997 estimate were not consistent with that used in this study, and may have been an underestimate). From 2003 to 2007, both MCR and KAR colony sizes increased by 152% and 153%, respectively. By 2007, MCR nesting Ross's geese were estimated to number 81,408, relative to 800,987 nesting at KAR (Alisauskas, unpublished data).

4.5.2 Components of Recruitment

From 2003–2007, Ross's geese arriving at MCR were able to initiate nests on average 7 days before those migrating to KAR, despite initiating nests 1 day later in 2004. Similarly, a late spring at MCR in 2004 affected both clutch size and nest success proportionally more than at KAR. Although Reed et al. (2004) suggest a southern nesting colony (MCR) would have a more stable climate than a northern colony (KAR) resulting in fewer non-productive years, from 2003–2007, nest initiation dates varied 23 days at MCR, but only 10 days at KAR. Additionally, MCR nest success varied by 26% in 3 years (2003–2005) and was lower than KAR in 2004. During the same period, KAR appeared more stable with nest success varying by only

14%. More stable estimates of nest success at KAR could be due to predator swamping due to geese acting as a large prey population. In late nesting years (2004), breeding propensity appeared to be depressed; considering MCR has 1/10th the breeding population, the relative influence that predators have on nest success of nesting populations should be greater than at KAR. Advantages of initiating nests earlier at MCR might be important to the growth and development of goslings. As MCR is farther south, the summer growing season will on average be longer, allowing more opportunity for goslings to grow and fledge. Despite possible chronological advantages of earlier nesting at MCR, factors unrelated to latitude such as access to quality brood rearing forage also influence recruitment. Although brood rearing habitat was not evaluated nor compared at either MCR or KAR, differences in quality and access to forage at this time can significantly affect gosling growth rates (Badzinski et al. 2002).

4.5.3 Survival

The estimate of 0.83 (*CL* = 0.73–0.90) for annual survival probability of adult Ross's geese at MCR was similar to geese marked at KAR during that same period, and to other arctic-nesting geese in general (Kirby et al. 1986, Francis et al. 1992, Ward et al. 1997, Alisauskas and Lindberg 2002, Menu et al. 2002, Alisauskas et al. 2006). Of variables considered, only age affected survival estimates, since adults survived at a rate more than twice that of hatch year birds. Despite proportionally different use of flyways, no

survival difference was detected between those marked at MCR and those marked at KAR. Survival estimates were also constant from 2002–2005; however, direct hunter recoveries declined slightly during the last two years of the study. Since hunters often fail to report a harvested goose until the next year, or even years later, data for direct recovery rate estimates can be incomplete. Depressed recovery rates for one or two years is not uncommon for that reason. Recoveries of Ross's geese were also greater for hatch year geese at both KAR and MCR, and greater at MCR than KAR for both adult and hatch year. Given that MCR is farther south, birds that nest there may reach the Prairies before those from higher arctic colonies, subjecting themselves to greater hunting pressure before being diluted by larger more northern populations. Additionally, with the inclusion of a spring conservation order and elevated fall bag limits, light goose hunting regulations within the Mississippi Flyway are more liberal than the Pacific Flyway. Although KAR Ross's geese are commonly harvested in Mississippi and Central Flyways, they have a greater proportional contribution to Pacific Flyway harvest than the Ross's geese from MCR (Figure 4.8). Given that differential recovery of Ross's geese marked at MCR and KAR did not influence survival estimates, it is apparent that mortality due to harvest at MCR, to at least this level, has been compensatory to overall mortality.

4.5.4 Breeding Propensity

Between 2004 and 2006, breeding propensity (± 95% CL) of neckbanded female Ross's geese at MCR varied from 50% (±14%) to 80% (±19%), and averaged 68% (±17%), confirming that temporary emigration from breeding populations is common. Temporary emigration has also been noted as common and variable in greater snow geese (*C. caerulescens atlantica*) (Reed et al. 2004), but low and consistent in Brant (*Branta bernicla nigricans*) (Sedinger et al. 2001) and lesser snow geese (Cooch et al. 2001). Breeding propensity among greater snow geese varied temporally, inversely correlated with spring temperature, and weakly correlated with timing of snowmelt (Reed et al. 2003). Similarly, breeding propensity of Ross's geese at MCR varied temporally and was low in 2004, when average May temperatures were considerably lower than the 20-year average. Overall, MCR estimates of breeding propensity may be biased low as results were acquired from only neckbanded birds. Reed at al. (2005) suggested that neckbanded females are more likely to emigrate temporarily from breeding areas, thereby reducing local breeding propensity (Menu et al. 2000, Schmutz & Morse 2000). Although southern colonies like MCR and LaPerouse Bay (Cooch et al. 2001) may not be subject to the extreme weather variations at high arctic colonies, breeding propensity still varies. It has been demonstrated by Ankney (1975), Craven (1979), Castelli and Trost (1996), Schmutz and Morse (2000), Alisauskas and Lindberg (2002), and Alisauskas et al. (2006) that most species of neckbanded geese have lower survival. But, survival differences were not found when evaluating

larger Canada geese (Samuel et al. 1990) and greater snow geese (Menu et al. 2000). Breeding propensity of neckbanded greater snow geese is potentially lower (Reed et al. 2005), but this relationship was not found in Ross's geese marked in QMG (Drake 2006). It is not known if apparent variation in breeding propensity at MCR is caused by the effects of the neckbands. Lastly, MCR Ross's goose breeding propensity data were based on 3 years. A longer study might produce different results.

Sustainability of MCR Ross's geese through *in situ* production alone can be assessed if I assume that demographic parameters are estimated correctly and that no net immigration occurs into the MCR colony each year. Population growth at MCR without net immigration from the central arctic can be expressed as:

$$\lambda = F + S \qquad \text{(Equation 1)}$$

where population growth rate ($\lambda = 1.114$) for 2003–2007 is a function of *per capita* female (*in situ*) recruitment (F) plus annual survival ($S = 0.830$). Rearranging this equation, we can determine the recruitment rate (F) necessary to result in a growth rate of 1.114, in the absence of immigration, as follows:

$$F = \lambda - S, \text{ or } F = 1.114 - 0.830 = 0.284. \qquad \text{(Equation 2)}$$

Recruitment can be expressed as:

$$F = 0.5 \times CS \times S_{egg} \times S_{gos} \times S_{juv} \times S_{ahy\ (1–2\ yrs)} \times BP \qquad \text{(Equation 3)}$$

where female recruitment ($F = 0.284$) is a function of the proportion of eggs that produce females (0.5), average clutch size (CS = 3.2), average egg

survival over the incubation period (S_{egg} = 0.70), gosling survival to fledge (S_{gos} = unknown [see below]), first year survival (S_{juv} = 0.38), annual adult survival to age of breeding where age of first breeding is assumed to be between 2 and 3 years, and breeding propensity. Although first year survival needs only to be estimated for 10 months, it was assumed that most mortality should occur during this period. Accordingly, I used the estimate of annual survival to represent survival probability during months 1–10. Estimated breeding propensity at MCR was 0.68, but this may be biased low as Reed et al. (2005) found that neckbanded greater snow geese were half as likely to nest as legbanded geese. For this exercise, I will assume non-neckbanded geese at MCR have a breeding propensity equal to 1.0. If we assume that half of females breed for the first time at 2 years and half at 3 years, adult survival probability to breeding age ($S_{ahy(1\text{-}2\ yrs)}$) will be one-half of 1 year's adult survival rate (0.83) plus one-half of 2 years' adult survival rate (0.83 × 0.83), or (0.83 x 0.50) + (0.83 x 0.83 x 0.50) = 0.76. After solving for the unknown (S_{gos}):

$S_{gos} = F\ (0.284) / (0.5 \times 3.2 \times 0.70 \times 0.38 \times 0.76 \times 1) = 0.88$ (Equation 3)

For the nesting colony to have grown at the annual rate observed (11.4%) without net immigration, gosling survival would have to have been 88% (but 129% with estimated breeding propensity of only 0.68).

Assuming net immigration, for MCR to be sustainable through *in situ* production alone, recruitment would need to be 0.17 (λ (1.00) – S (0.83)). Substituting 0.17 for F in Equation 3 results in expected gosling survival to

fledging of 53% (77% with estimated breeding propensity of 0.68). Gosling survival estimates for lesser snow geese at La Perouse Bay, Manitoba ranged from 67%–70% (Rockwell et al. 1997). Assuming breeding propensity of non-neckbanded geese is near 1.0, data from this study suggest that MCR may have been able to grow, at least in part through *in situ* production alone.

Drake (2006) concluded that tens of thousands of geese moved each year within the QMG and that growth of the 2 largest nesting colonies (KAR and Colony 10) depended on immigration from smaller colonies. It is possible that MCR is similarly dependent on immigration to support its growth, despite evidence of significant, but male-biased movement from MCR to QMG (Drake 2006). Brawn and Robinson (1996) have demonstrated that persistence of sub-populations of neo-tropical migrant songbirds can be unrelated to local productivity. These sub-populations can act as sinks, persisting or growing based primarily on immigration.

Understanding the relationship between population trends and demographic processes such as recruitment and dispersal (immigration, emigration) is fundamental for conservation and management (Pullian and Danielson 1991). It appears that the MCR colony of Ross's geese could sustain itself without the substantial contribution of immigrants from the main North American breeding populations in Canada's central arctic regions (i.e., south of Queen Maud Gulf) (Ryder and Alisauskas 1995).

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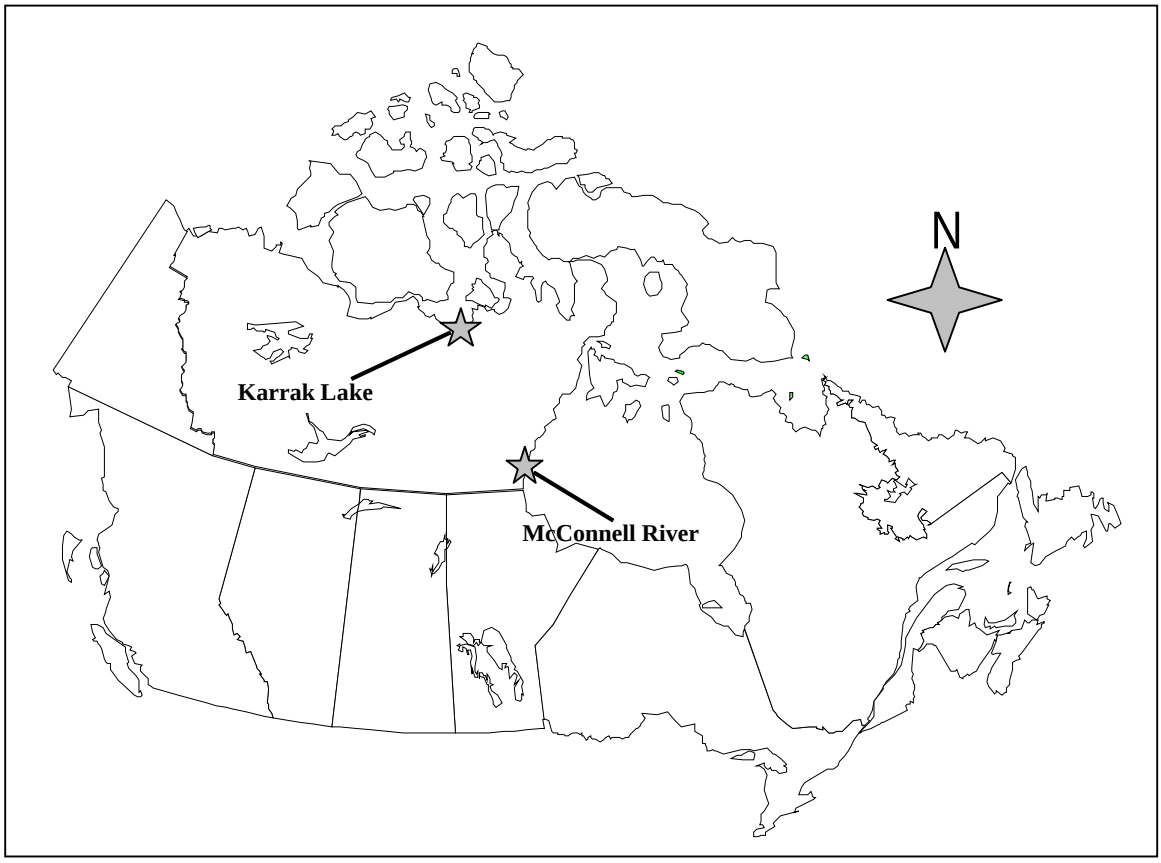

Figure 4.1. General locations of McConnell River and Karrak Lake Ross's goose colonies.

Table 4.1. MCR Ross's goose nest density, nest detection, and colony area (± 95% CL), 2003–2007.

	2003	2004	2005	2006	2007
Density (*D*)	2680	1824	2001	2183	2230
D l.c.l.	1853	1356	1466	1581	1566
D u.c.l.	3875	2455	2730	3013	3176
Detection (*p*)	1.00	1.00	1.00	0.82	0.74
p l.c.l.	1.00	1.00	1.00	0.66	0.60
p u.c.l.	1.00	1.00	1.00	1.00	0.92
Area	10.00	15.75	17.25	18.75	18.25

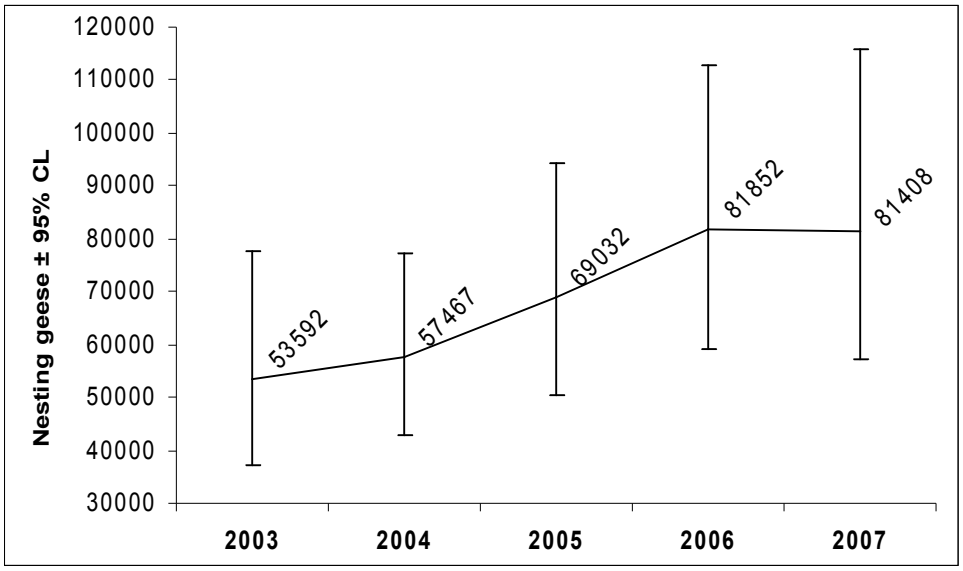

Figure 4.2. MCR nesting population estimate (± 95% CL) for Ross's geese, 2003–2007.

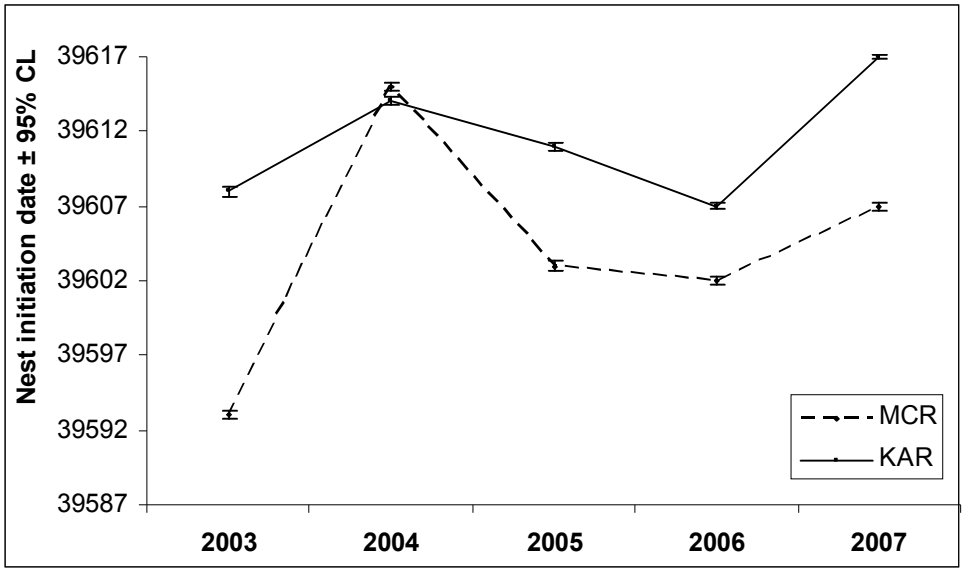

Figure 4.3. Mean annual nest initiation dates (± 95% CL) at MCR and KAR, 2003–2007.

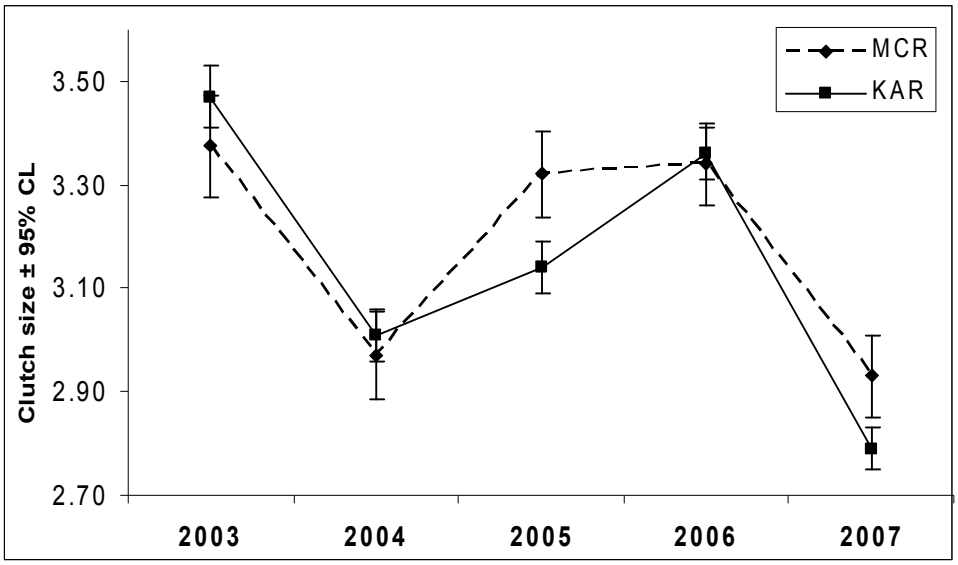

Figure 4.4. Mean annual clutch sizes (± 95% CL) at MCR and KAR, 2003–2007.

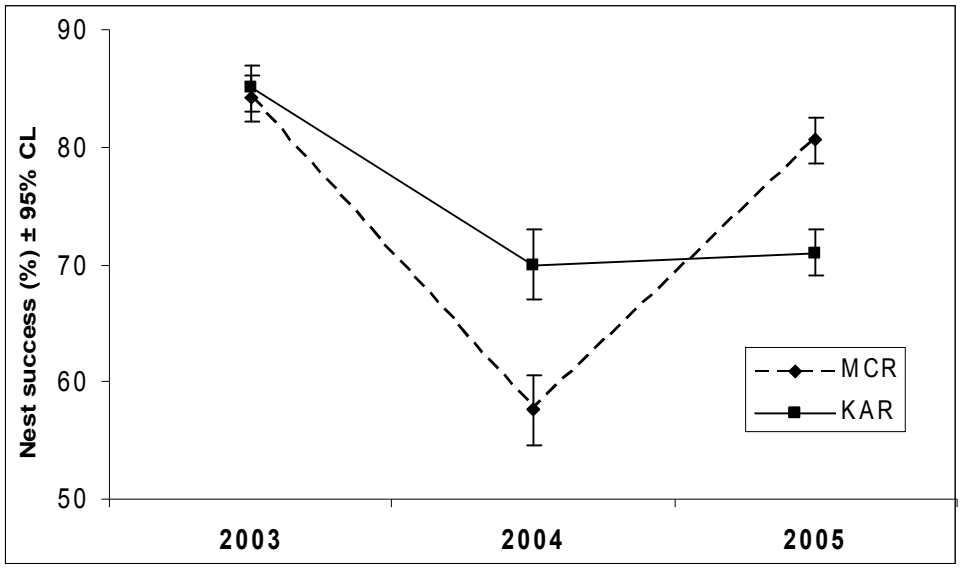

Figure 4.5. Mean annual apparent nest success (± 95% CL) at MCR and KAR, 2003–2005.

Table 4.2. Model structure, $QAIC_c$, $\Delta QAIC_c$, model weight (ω_{QAICc}), number of parameters (*K*), and deviance of models used to estimate effects of colony, age, and year on survival (*S*) and recovery (*f*) probabilities of Ross's geese marked at QMG or MCR, 2002–2006.

Model	QAICc	ΔQAICc	ω_{QAICc}	*K*	QDeviance
S (a) *f* (c+a+T)	9289.22	0.00	0.53	6	63.16
S (a) *f* (c+a+t)	9290.63	1.41	0.26	9	58.57
S (c+a) *f* (c+a+t)	9292.15	2.93	0.12	10	58.09
S (c+a+T) *f* (c+a+t)	9293.95	4.73	0.05	11	57.89
S (c+a+t) *f* (c+a+t)	9295.09	5.87	0.03	13	55.02
S (c+a*T) *f* (c+a+t)	9297.82	8.60	0.01	14	55.75
S (c*a*t) *f* (c*a*t) S 2-way only	9298.69	9.47	0.00	33	18.57
S (c*a*t) *f* (c*a*t) c+a additive	9300.59	11.37	0.00	27	32.49
S (c*a*t) *f* (c*a*t) global model	9301.15	11.93	0.00	36	15.02
S (a) *f* (c+a)	9305.65	16.43	0.00	5	81.59
S (c*a*t) *f* (c*a*t) f 2-way only	9307.02	17.81	0.00	32	28.91
S (c*a*t) *f* (c*a*t) 2-way only	9311.59	22.38	0.00	29	39.49
S (c+a) *f* (a+t)	9315.08	25.86	0.00	9	83.02
S (a) *f* (a+t)	9317.85	28.63	0.00	8	87.79
S (c*a*t) *f* (c+a+t) c+a additive	9320.42	31.21	0.00	18	70.35
S (c*a*t) *f* (c+a+t)	9321.76	32.55	0.00	20	67.69
S (c+a*t) *f* (c+a*t)	9323.32	34.11	0.00	20	69.24
S (c+a) *f* (c+a)	9331.28	42.07	0.00	6	105.22

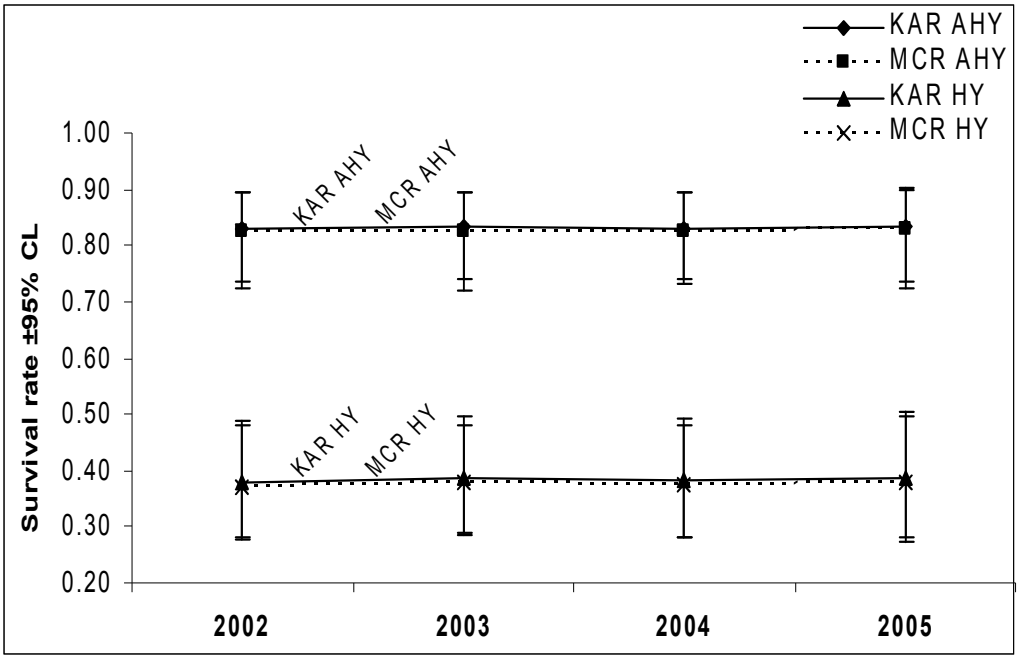

Figure 4.6. MCR and KAR Ross's goose survival estimates (± 95% CL) by colony and age, 2002–2005.

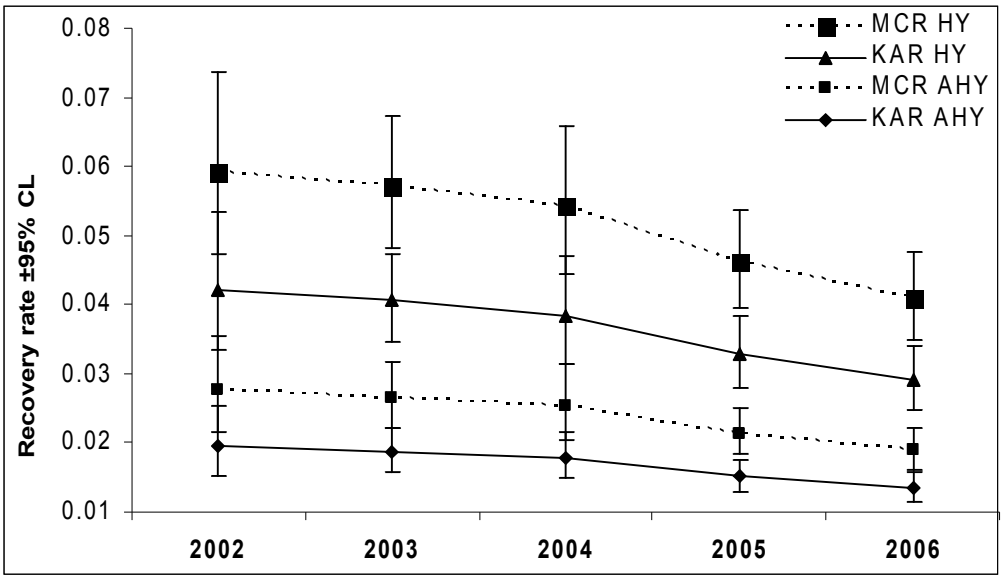

Figure 4.7. MCR and KAR Ross's goose recovery estimates (± 95% CL) by colony and age, 2002–2006.

Table 4.3. Model structure, $QAIC_c$, $\Delta QAIC_c$, model weight (ω_{QAICc}), number of parameters (*K*), and deviance of models used to estimate effect of year on probabilities of apparent survival (Φ), temporary emigration (γ) and detection (*p*) of marked Ross's geese at MCR, 2003–2006.

Model	QAICc	ΔQAICc	ω_{QAICc}	*K*	QDeviance
Φ (.) γ (t) p (t)	2034.61	0.00	0.94	7.00	5849.92
Φ (.) γ (t) p (.)	2041.15	6.54	0.04	5.00	5860.47
Φ (.) γ (.) p (.)	2042.82	8.21	0.02	3.00	5866.15
Φ (.) γ (.) p (t)	2044.64	10.02	0.01	6.00	5861.95

Table 4.4. Model averaged estimates of apparent survival, breeding propensity (1-γ), and detection probabilities ± SE and 95% CL for neckbanded geese nesting at MCR, 2003–2006.

Parameter	Estimate	SE	LCI	UCI
Apparent Survival	0.73	0.04	0.64	0.80
Breeding propensity 2004	0.50	0.09	0.32	0.67
Breeding propensity 2005	0.75	0.10	0.51	0.90
Breeding propensity 2006	0.80	0.12	0.47	0.94
Detection 2003	0.42	0.05	0.33	0.52
Detection 2004	0.46	0.05	0.36	0.57
Detection 2005	0.43	0.04	0.35	0.51
Detection 2006	0.30	0.04	0.23	0.37

CHAPTER 5. SYNTHESIS: POPULATION BIOLOGY OF ROSS'S GEESE AT McCONNELL RIVER

5.1 PIONEERING A NEW COLONY: CAUSE AND CONSEQUENCE

Ross's geese (*Chen rossii*) nesting in the eastern arctic have continued to increased greatly in abundance since they were discovered in large numbers in 1994 (Kerbes et al. 2006). Because population estimates of these Ross's geese have been unavailable since 1997 (Kerbes et al. 2006), one objective of this study was to develop baseline information on this new and potentially growing population nesting in Canada's eastern arctic. A random event such as heavy winds or a spring snow storm may have been responsible for this large scale dispersal event. Considering that MCR was traditionally a large lesser snow goose (*Chen caerulescens caerulescens*) colony, it is possible that flocks of Ross's geese followed the snow goose migration to MCR.

Assuming that immigration from Canada's central arctic colonies is in part contributing to the expansion of Ross's geese at McConnell River, I attempted to determine if nesting in Canada's eastern arctic was advantageous. Differences in survival of Ross's geese from the McConnell River (MCR) and Queen Maud Gulf (QMG) migratory bird sanctuaries were compared, in addition to nesting indices such as laying date, clutch size, and nest success.

A survival advantage, possibly due to longer summers compared to those at QMG, was not detected for MCR Ross's geese. However, birds

initiating nests at MCR did so earlier (~7 days) and with more fat and protein than those at QMG. An energetic advantage may have influenced MCR geese to lay larger clutch sizes in 2 of 5 years and no fewer than the QMG geese in the remaining 3 years. If nutrient reserves played a role in nest constancy and reduce exposure to predators, it was undetectable since overall nest success between 2003 and 2005 was similar between locations.

As individual fitness is often influenced by habitat quality, isolating variables that contribute to habitat selection increases our understanding of how temporary and permanent movement decisions are made. Decisions pertaining to nesting dispersal were investigated in Chapter 3. Nesting success of both focal animals and their nearest neighbours the previous year was evaluated as a variable that might influence breeding propensity, as well as between-year movement within the MCR colony. A female's previous nest success did not appear to be important when choosing if and where to nest in subsequent years, nor did the success of her neighbours. Similar to what Lepage et al. (2000) found with greater snow geese (*Chen caerulescens atlantica*) urgency appeared to be a selective force since production was greatest in years when nesting was early. Accordingly, nest sites that are available (clear of snow) may be more valuable than nearby snow-covered nests used by successful females the previous year.

On a larger scale, dispersal of Ross's geese to the eastern arctic may have been similarly motivated (i.e., based on habitat quality) (Doligez et al. 2002). If high-quality habitat was motivation for Ross's geese to disperse to

MCR in 1994, it was inconsistently reflected in clutch size alone. Alternately, Lidicker (1962) suggested that dispersal to new breeding colonies can be motivated in animals from habitats that are above carrying capacity. It does not appear likely that Karrak Lake (KAR) was at or near carrying capacity when Ross's geese pioneered MCR in 1994, as the nesting population of Ross's geese at KAR has since increased 400% (Alisauskas, unpublished data). Alternately, at this scale it is plausible that Ross's geese have been dispersing eastward in a way that is consistent with Fretwell and Lucas's ideal free distribution (IFD) hypothesis (1970). If geese are able to accurately evaluate habitat and move freely from one site to another, fitness of individuals occupying either habitat would be similar. As fitness of Ross's geese at KAR and MCR do appear similar, it is possible that geese are settling according to an IFD at a landscape scale.

As the population of Ross's geese continued to grow within the Queen Maud Gulf, the continental population expanded eastward, a trend that was identified over 40 years ago (Dzubin 1965). Inconsistent with Fretwell's hypothesis that individuals only interact with each other to compete for resources, the original movement of Ross's geese to new habitat at MCR was as a large colonizing group (~10,000). Similar to sheep (Michelena et al. 2009), there appears to be an advantage for geese to stay in groups, but at high density, individuals face a trade-off between maximizing their access to a preferred habitat and staying with the group. The IFD hypothesis suggests that habitats of better quality would be occupied first. For example,

pied flycatchers (*Ficedula hypoleuca)* fill large woodlots to a threshold before smaller woodlots are used (Huhta et al.1998). Similarity, Ross's geese did not spill into the eastern arctic in substantial numbers until the mid 1990's, when then central arctic population was at a record high level. Nicolai et al. (2008) described how movement from a major breeding colony resulting in a major decline in nesting density may not be initially advantageous.

Fretwell and Lucas (1970) further developed the "Allee-type" ideal free distribution model that deserves consideration when evaluating movement of colonial nesting geese. In this case, the suitability of habitat at the new colony (MCR) will increase with increasing local density while concurrently; the suitability of KAR will decrease with increasing density. This can be explained by inverse density-dependence in small groups. Densities below a certain threshold may result in greater risk of individuals to predation and stochastic weather events. As in Black-legged Kittiwake (*Rissa tridactyla*) (Kildaw et al. 2005), benefits of colonial nesting can result in rapid initial growth of new nesting colonies, often fueled primarily by immigration.

Regardless of the cause of pioneering, the resulting population at MCR has persisted since 1994 and is growing at an annual rate (>11%) similar to that estimated at KAR (Chapter 4).

Dispersing to new nesting areas involves risk (Belichon et al. 1996, Fahrig 2007) and MCR Ross's geese have endured different predator communities (MacInnes 1962, Samelius 2004) and increased harvest

pressure by humans (Chapter 4). Considering that population growth estimated from 1994–1997 (Kerbes et al. 2006) was similar to that estimated from 2003–2007 (Chapter 4) and nest densities were small relative to KAR, MCR appears stable and potentially able to support significant further growth.

Lastly, dispersal to breeding areas in the eastern arctic (Kerbes et al. 2006) coincided with an eastward shift in migration (Dzubin 1965, Alisauskas et al. 2006) and wintering areas (Ryder and Alisauskas 1995). This eastward movement of nesting Ross's geese is concurrent with an eastern shift in proportional Ross's goose recovery rates. Alisauskas et al. (2006) suggested that greater harvest in Central and Mississippi Flyways combined with lower harvest in Pacific Flyway may result in subpopulation differences in survival. Although I did not detect a difference in survival between the two nesting colonies, differences such as timing of movement, nutritional load on arrival, and nesting vital rates vary regionally. Nesting at MCR appears to carries both advantages (e.g. earlier nest initiation) and disadvantages (e.g. variable nest success), relative to KAR. Regardless, Ross's geese appear able to exploit new environments by dispersing long distances and nesting successfully in new locations. Given the high sociality of Ross's geese leading to mixing on migration and wintering areas, and the propensity for movement between nesting areas (Drake 2006), perhaps it is not surprising that this broad scale equilibrium exists.

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APPENDIX. EFFECT OF NECKBAND COLOUR ON SURVIVAL AND RECOVERY RATES OF ROSS'S GEESE

A.1 ABSTRACT

Coloured neckbands are known to reduce survival rates of geese, but the underlying cause for lower survival is unknown. I tested the hypothesis that hunters cause this lower survival rate by actively targeting neckbanded geese. I evaluated this hypothesis by estimating recovery and survival rates of adult Ross's geese (*Chen rossii*) at both Queen Maud Gulf (QMG) and McConnell River (MCR) migratory bird sanctuaries carrying each of four marker types: 1) standard legbands (LB, *n* = 11,321) for basic estimates of direct recovery and survival rates; 2) reward-legbands (RB, *n* = 5,893) to account for differences with markers that elevate reporting rates; 3) coloured neckbands (CB, *n* = 8,587) as the marked sample most vulnerable to detection and potential targeting by hunters; and 4) white neckbands (WB, *n* =6,501)) as the sample exposed to the general risks of carrying neckbands but only minimally detectable by hunters, if at all. At both QMG and MCR, direct recovery rates of Ross's geese were lowest for those marked with legbands and highest for those marked with neckbands. Geese with reward-legbands were recovered at an intermediate rate between those marked with legbands only and neckbands. As predicted, survival rate estimates for geese with neckbands were lower than for those marked with legbands only. However, rates were similar between geese marked with coloured (0.53) and white (0.53) neckbands, and lower than those marked

with either standard legbands only (0.77) or with reward-legbands (0.78). Neckbanded geese were recovered at much higher rates than the geese marked with both legbands only and reward-legbands. Ross's geese harvested and retrieved with standard legbands were estimated to be reported at a rate of 0.85 (Zimmerman et al. *in press*). Since reward-legbands increase reporting rate significantly (1.0 at $60), there is little support that recovery rates of neckbanded geese marked at KAR and MCR (0.035 and 0.040, respectively) can be explained by reporting rates ~40% greater than that of reward legbanded geese. "Invisible" markers were recovered at rates similar to those for coloured markers, suggesting that hunter selection of coloured neckbanded geese did not contribute greatly to lower survival rates in neckbanded geese. Rather, results suggest that neckbanded birds, regardless of neckband visibility are more vulnerable to hunters than geese marked only with legbands.

A.2 INTRODUCTION

Neckbands are often used in goose research because they are highly visible and permit individual identification of geese from greater distances than if they are marked only with standard metal legbands. Hence, neckbands can be a useful for estimating vital rates of goose populations, but their use for unbiased estimation of different vital rates such as survival several assumptions need to be met. These include: 1) all animals in the population at the time of capture are captured with equal probability, 2) all animals

survive with equal probability, 3) survival and capture of an animal is independent of the survival and capture of all other animals, 4) captured animals and previously uncaptured animals survive equally well, and 5) all banded geese retain their bands and are correctly identified (Pollock et al. 1990). If such assumptions are violated use of neckbands can lead to incorrect biased estimates of vital rates and incorrect inferences about population biology. For example, increased mortality of study animals carrying neckbands has been suspected or demonstrated in nearly every North American species of goose (Ankney 1975, Craven 1979, Castelli and Trost 1996, Schmutz and Morse 2000, Alisauskas and Lindberg 2002, Alisauskas et al. 2006, but see Reed et al. 2005). A primary assumption of mark-recapture studies is that the mark itself does not influence survival. Alisauskas et al. (2006) showed that neckbands reduced survival estimates in Ross's geese (*Chen rossii*) from 1989–2001. However, bias can be measured and used to correct biased estimates (Alisauskas and Lindberg 2002).

How neckbands affect survival is also important because factors that influence survival may also bias estimates of immigration and emigration. A clearer understanding of the mechanisms that reduce survival of neckbanded geese will aid in bias-correction of survival estimates.

Three general hypotheses for reduced survival of geese marked with neckbands include:

(1) Icing—Greenwood and Bair (1974) noted the formation of ice on neckbands of Canada geese (*Branta canadensis*) during winter storms. Zicus et al. (1983) also concluded that high winds in addition to cold temperatures contributed to neckband icing in Canada geese, which often resulted in mortality;

(2) Energetics—During nesting, Ankney (1975) estimated that neckbanded lesser snow geese (*Chen caerulescens caerulescens*) at the McConnell River Migratory Bird Sanctuary (MCR) were >5 times more likely to starve while incubating nests than those without neckbands. This was thought to result from neckbanded females spending less time feeding because of the increased time spent nibbling on and scratching at their neckbands. Schmutz and Morse (2000) agreed that the negative effects of neckbands are likely due to increased energetic demands. They further speculated that neckbands negatively influence both thermodynamics and aerodynamics resulting in increased mortality;

(3) Neckband hunting—Relative to legbands, neckbands are designed to be detectable from a distance of several hundred meters, so they are large and conspicuously coloured. Some hunters may exploit this increased detectability of neckbands and select geese so marked for harvest. It is unknown if this is a common practice, but if active selection of neckbanded geese is widespread, recovery rates and

possibly survival rates of those marked with neckbands can be affected negatively.

I marked Ross's geese with a neckband specifically designed to reduce detectability by hunters; this was done in conjunction with highly visible neckbands that are normally used for other purposes that require individual identification. I tested the hypotheses that coloured neckbands result in increased recovery rates and reduced survival rates of adult Ross's geese compared to those that are difficult to detect by hunters. To do this, I compared recovery and survival rates of Ross's geese marked with neckbands that were either conspicuously coloured or completely white and virtually invisible to the naked eye when carried by white-plumaged geese, such as Ross's geese. I also used a sample of geese marked with legbands and reward-legbands to account for any potential differences in band reporting probability that might be associated with marker type.

A.3 METHODS

A.3.1 Study Area

Ross's geese were marked within or near the McConnell River (MCR) or Queen Maud Gulf (QMG) Migratory Bird Sanctuaries (Figure A.1). More than 90% of all Ross's geese nest within QMG, while the MCR nesting colony is the largest known concentration outside of the central arctic (Moser 2001).

A.3.2 Field Methods

Methods used to estimate survival and recovery rates of adult Ross's geese relied on band-recoveries from birds shot by hunters. If all birds harvest were reported, the proportion of birds banded that were reported would be the harvest rate. Considering not all harvested birds are reported, harvest rate equals the recovery rate adjusted for band reporting rate (Henny and Burnham 1976).

Flightless molting adult Ross's geese were corralled into nets using a helicopter following methods described by Cooch (1954) and Timm and Bromley (1976) in early August (2003–2005) at QMG brood-rearing areas. During the same period, helicopters, as well as all terrain vehicles (ATV: Honda Foreman 450), were used to capture geese at MCR. While using ATVs, researchers drove along the Hudson Bay coast in search of large brood-rearing flocks (200–400 adults). When located, geese were held in position by two ATVs that advanced quickly on either side of the flock. A third ATV (with drive net) searched for a suitably dry banding area nearby. Once the third researcher set up the drive net, geese were guided at walking speed toward the net using the two ATVs. Once near the net, all three researchers walked the geese into the net on foot.

All geese received a standard USFWS/CWS metal legband. Additionally, each goose was given one of four treatments: (1) reward-legbands—geese marked and recovered with a reward-legband have a reporting rate greater than those marked with legbands only (Zimmerman et al., *in press*).

Although reporting rate of geese marked with neckbands has yet to be estimated, neckbanded geese may be reported at greater rates than geese marked with only legbands. As well, reporting rate of neckbanded geese may approach or equal that of reward banded geese, but should not exceed it because reward bands solicit hunters to report bands with a monetary reward (Henny and Burnham 1976). With current leg bands (1-800 telephone number) reporting rates for Ross's geese are ~85% but a monetary reward of $60 ensured >99% (Zimmerman et al. *in press*). This allowed me to account for potential differences in reporting rates that might be associated with marker type; (2) yellow neckbands with black alphanumeric codes, or blue neckbands with white codes; (3) white neckbands with white codes; and (4) only the standard legband (control), to estimate the amount by which recovery was increased and survival reduced due to neckband presence. Detection probability of white neckbands relative to coloured neckbands by numbers could not be readily estimated; however, detection estimates from collar reading with spotting scopes from distances of 40 m to 400 m at MCR suggested that detection probability of white neckbands was immeasurably low, i.e., $\hat{p}$ <0.001 and they were far more difficult to detect than yellow neckband with engraved black codes ($\hat{p}$ = 0.61–0.66 (J. H. Caswell, unpublished data). While marking geese, neckband treatments (coloured vs. white) were alternated every 50 birds, while legbands (reward and control) were alternated with every bird to conform to USFWS/CWS protocol. Recovery data for birds marked during

this period were obtained from the Bird Banding Laboratory in Laurel, Maryland.

I predicted that: (1) geese with coloured neckbands would have higher recovery rates and lower survival rates than those with white neckbands, both resulting from an inferred increase in harvest rate, and that this would be consistent with the hypothesis that hunters were actively selecting geese with coloured neckbands; (2) reward-legbanded birds would have the highest recovery rates of all 4 experimental groups; (3) birds with coloured neckbands would have higher recovery rates and lower survival than those with legbands only (again consistent with active selection by hunters); and (4) birds with white neckbands would have recovery rates similar to those of birds with legbands only (because hypothetically they would not be actively selected by hunters), otherwise higher recovery rates of geese with white neckbands would strongly suggest that they are more likely to suffer greater exposure to hunters perhaps because of their greater likelihood to approach decoys.

A.3.3 Statistical Analyses

I estimated direct recovery ($\hat{f}_i$) and annual survival ($\hat{S}_i$) probabilities using Brownie et al. (1985) models in program MARK (White and Burnham 1999). Models were constructed *a priori* and included the following: (1) Time dependent (yr) and constant survival and recovery rates. (2) Effect of banding location (loc; QMG vs. MCR), whereby estimates of recovery and

survival rates may vary between QMG and MCR nesting colonies. Sources of variation may relate to differences in migration distance and proportional use of different flyways in which harvest regulations vary. Additionally, marking locations were separated by over 800km so that differences in survival may relate to regional differences in weather, disease, or other unmeasured effects. (3) Marker type (legband (LB) vs. reward-legband (RB) vs. coloured neckband (CB) vs. white neckband (WB)). To test for active selection of neckbands by hunters, models in which CB and WB recovery and survival rates were estimated separately were compared to models in which estimates were pooled. RB recovery rates were used to account for reporting rate bias with legbanded individuals. I compared quality of models in which recovery and survival rates were estimated for LB separately from NB, with models in which estimates were pooled for these two groups. Data were pooled by sex as annual survival does not appear to vary significantly between sexes in Ross's geese (Melinchuk and Ryder 1980). Goodness-of-fit of the global model {*S* (yr*loc*lb*rb*cb*wb) *f* (yr*loc*lb*rb*cb*wb)} was tested using 100 parametric bootstrap simulations with program MARK. Deviance calculated from data was greater than 95% of the simulated deviances, suggesting a lack of model fit. A variance inflation factor of $\hat{c}$ = 1.2903 was estimated and used to adjust variance estimates. Akaike's Information Criterion (AIC), adjusted for small sample size (AIC_c) and overdispersion ($QAIC_c = AIC_c / \hat{c}$), was used to select the best from among all competing models. Models within $\Delta QAIC_c < 2$ were considered

competitive and parameter estimates were averaged across the entire model set using model weights to account for model uncertainty (Burnham and Anderson 2002), and are presented as maximum likelihood estimates (± 95% CL).

A.4 RESULTS

From 2003 to 2005, 32,302 adult Ross's geese were marked with standard metal USFWS/CWS legbands at QMG and MCR (16,655 and 15,647, respectively). Of these, 11,321 received no additional markers, but another 5,893 geese marked with metal legbands also received a reward-legband, and another 8,587 also received a coloured neckband, while a final group of 6,501 also received a white neckband (Table A.1).

A.4.1 Recovery Probability

The most parsimonious model of variation in recovery probability, hereafter *recovery* (ωQAICc = 0.61) included effects of location and marker type. Ninety-five % CL of recovery for legbanded, reward-legbanded, and neckbanded (CB & WB) geese were different from one another. However, recoveries of coloured and white neckbanded geese were similar (Figure A.2). This model was 2.8 times better supported by the data than the next best model ($\Delta QAIC_c = 2.05$), which structured variation in recovery among all 4 treatment groups, i.e. coloured and white neckbanded geese separately (Table A.2). Model-averaged parameter estimates (± 95% CL) suggested

that direct recovery (x100%) was lowest for LB (1.7% ± 0.3, and 2.4% ± 0.4, for QMG and MCR, respectively) and greatest for NB (3.5% ± 0.5, and 4.0%–4.2% ± 0.6, for QMG and MCR) (Table A.3). Estimates for RB were intermediate between LB and NB treatments, and marker effect size (e.g., CB vs. WB, NB vs. LB) appeared similar at each site (Figure A.2).

A.4.2 Survival

The 3 best models (cumulative ωQAICc = 0.92) did not include an effect of neckband colour (CB vs. WB), while all top models (cumulative ωQAICc = 1.00) included an effect of neckband presence (LB & RB vs. CB & WB) (Table A.3). Although survival of geese marked with legbands was greater than those marked with neckbands, there was no detected effect of year or location (Figure A.3). Survival estimates (± 95% CL) of geese marked with neckbands (CB & WB) were 0.53 ± 0.07, whereas those marked with legbands were 0.77–0.78 ± 0.11 for LB and RB (Table A.3). Thus, neckband presence doubled the mortality rate of geese (0.47) compared to those that were marked only with legbands (0.23).

A.5 DISCUSSION

Direct recovery rates of Ross's geese were higher at MCR than QMG regardless of marker type. Although hunters recovered similar proportion of neckbanded and legbanded Canada geese marked at MCR (MacInnes and Dunn 1988) Ross's geese marked with neckbands were recovered at

greater rates than those marked with legbands and reward-legbands. Zimmerman et al. (*in press*) established that reporting rate estimates of LB Ross's geese was 85%. Given that reporting rate estimates of RB geese was greater than LB geese, and recovery of NB geese in this study was ~40% greater than that of RB geese, then recovery rate estimates of NB Ross's geese can be accounted for by elevated reporting rates alone. Higher recovery of NB geese relative to both LB and RB, for the most part, had to have been the result of increased vulnerability to hunters. Moreover, recovery of WB vs. CB was indistinguishable despite large differences in detection of each color type, thus hunters were unable to distinguish between WB and CB in this sample, despite the much greater visibility of CB compared to WB geese. I infer that hunters normally are unable to do so under the most common hunting conditions. Thus, I conclude that past reports of increase vulnerability of NB geese compared to LB geese (Alisauskas et al. 2006) was related to an effect of the collar on goose behaviour, whereby neckbanded geese are more predisposed to be attracted to hunters, who passively harvest such birds, rather than any active selection of such birds by hunters.

The mortality effect of neckbands were very similar to that estimated by Alisauskas et al. (2006), despite the fact that years of study did not overlap, and suggests that such effects of neckbands with this design are certain to occur. As well, the negative effect of neckbands on goose survival reported herein and elsewhere must have been an outcome of debilitating effects on

study animals rather than the ability of hunters to discern and selectively remove them from the sample because of a desire to acquire such birds.

The effect of location on recovery rate estimates (MCR > KAR) and survival rate estimates (MCR= KAR) for all marker types mirrors results from geese marked with only legbands over a longer period (Chapter 4). Assuming reporting rates were similar for geese harvested at MCR and KAR, the additional harvest of Ross's geese at MCR was mostly compensatory to other (non-hunting) forms of mortality.

There is anecdotal evidence, from internet discussion and the resale market, that geese with colored neckbands normally used in research are considered to be trophies by some hunters. Although there undoubtedly is some active selection of such trophies, its pervasiveness could not have been very great and apparently played no measurable role in elevated recovery of NB compared to LB geese. Most geese shot by hunters were probably identified as being neckbanded only after they were shot.

NB geese apparently were more vulnerable to hunters than LB geese because NB geese behaved in such a way that they had a higher likelihood of approaching or encountering hunters. Such altered behaviour may have resulted from diminished nutritional condition of NB geese (perhaps because of greater flight costs, or reduced time feeding) predisposing them to perhaps fly lower or be attracted to decoys, within shooting range of hunters. Weatherhead and Greenwood (1981) proposed a condition bias hypothesis where by birds in poor condition may have greater vulnerability to hunters

using decoys. The condition bias hypothesis has much empirical support from studies done with ducks (Greenwood et al. 1986, Hepp et al. 1986, Reinecke and Shaiffer 1988, Dufour et al. 1993, Heitmeyer et al. 1993), and is probably even more relevant to arctic-nesting geese that appear to rely heavily on nutrient reserves (Alisauskas and Ankney 1992, Alisauskas 2002). However, in the only known test of this hypothesis in geese, Morez et al. (2000) were unable to detect a condition bias in hunter shot or bait trapped greater snow geese (*Chen caerulescens atlantica*).

There is little doubt that there is measurable but unknown mortality due to non-hunting factors that are directed towards neckbanded geese. Icing, increased energetic and thermodynamic costs, and increased risk of predation warrant further investigation into their contribution to reduce survival in Ross's geese and other goose species.

The reliability of inferences drawn from use of neckbanded birds depends on the population parameter estimated. Although both recovery and mortality appear positively biased in neckbanded Ross's geese (Alisauskas et al. 2006), there were no effects detected on either correlates (e.g., nest initiation date), or components (e.g., breeding propensity, clutch size and nest success) of recruitment (Drake 2006). Nevertheless, the importance of questions that require use of neckbands needs to be balanced against the negative effects on inference power resulting from positive bias in mortality and recovery bias associated with them

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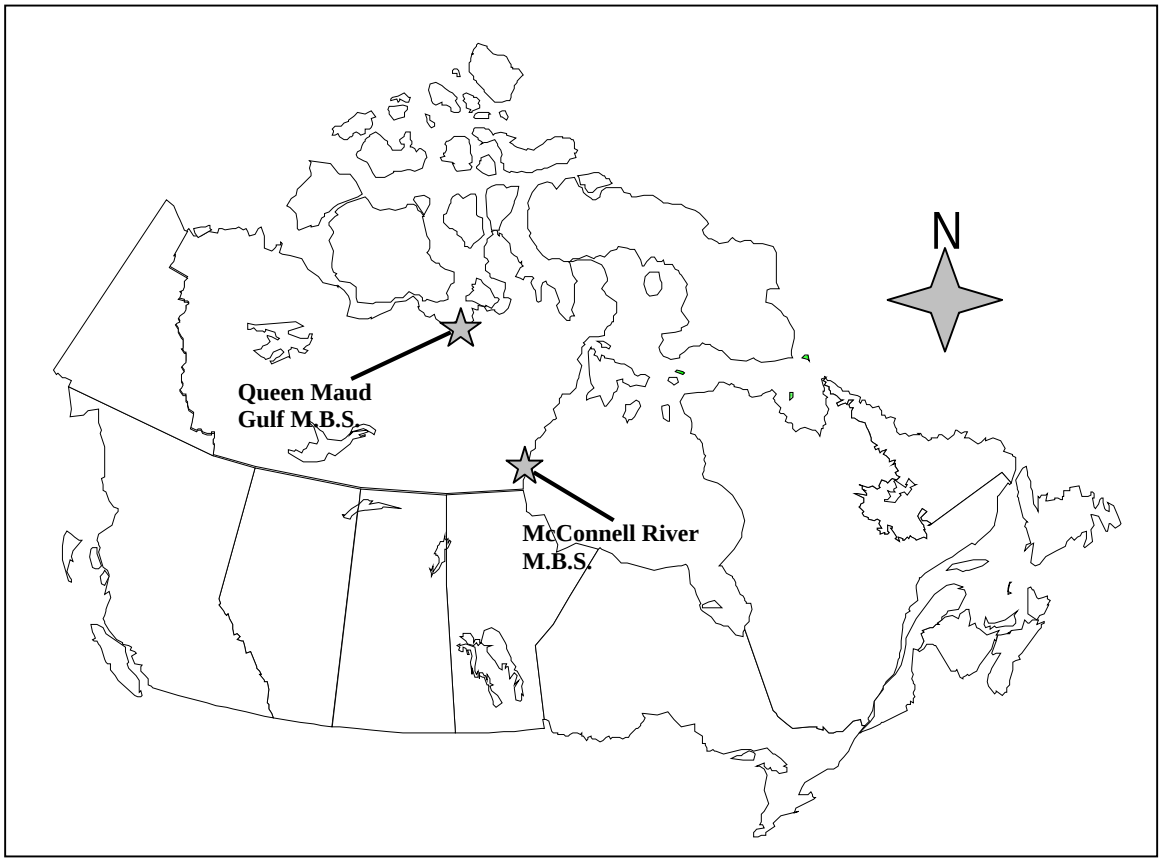

Figure A.1. General locations of McConnell River and Queen Maud Gulf migratory bird sanctuaries.

Table A.1. Number of Ross's geese marked and recovered from 2003 through spring 2006, by marker type and nesting colony.

Location	Marker	# Marked	# Recovered
McConnell River	legband only	4544	128
	legband + reward-legband	2899	150
	legband + coloured neckband	4702	283
	legband + white neckband	3502	173
Queen Maud Gulf	legband only	6777	185
	legband + reward-legband	2994	125
	legband + coloured neckband	3885	210
	legband + white neckband	2999	145

Table A.2. Model structure, $QAIC_c$, $\Delta QAIC_c$, model weight (ω_{QAICc}), number of parameters (*K*), and deviance of models used to estimate effects of year, colony, and marker type on survival (*S*) and recovery (*f*) parameters of Ross's geese marked at QMG and MCR, 2003–2005.

Model	QAICc	ΔQAICc	ωQAICc	*K*	QDeviance
S (lb=rb*cb=wb) *f* (loc*lb*rb*cb=wb)	10382.69	0.00	0.61	8	32.57
S (lb=rb*cb=wb) *f* (loc*lb*rb*cb*wb)	10384.74	2.05	0.22	10	30.61
S (lb*rb*cb=wb) *f* (loc*lb*rb*cb*wb)	10386.45	3.75	0.09	11	30.32
S (lb*rb*cb*wb) *f* (loc*lb*rb*cb*wb)	10388.41	5.72	0.04	12	30.28
S (lb=rb*cb=wb) *f* (loc*lb=rb*cb=wb)	10390.30	7.61	0.01	6	44.18
S (lb=rb*cb=wb) *f* (lb*rb*cb=wb)	10391.62	8.92	0.01	5	47.49
S (lb=rb*cb=wb) *f* (lb*rb*cb*wb)	10391.97	9.28	0.01	6	45.85
S (lb*rb*cb*wb) *f* (lb*rb*cb*wb)	10391.97	9.28	0.01	6	45.85
S (loc*lb*rb*cb*wb) *f* (loc*lb*rb*cb*wb)	10393.81	11.12	0.00	16	27.67
S (lb=rb*cb=wb) *f* (loc*lb*rb=cb=wb)	10393.81	11.12	0.00	6	47.69
S (lb*rb=cb=wb) *f* (loc*lb*rb*cb*wb)	10396.98	14.29	0.00	10	42.85
S (lb=rb=cb=wb) *f* (loc*lb*rb*cb*wb)	10399.24	16.55	0.00	9	47.12
S (yr*loc*lb*rb*cb*wb) *f* (yr*loc*lb*rb*cb*wb)	10423.59	40.90	0.00	40	9.37

Table A.3. Model averaged estimates of survival (*S*) and recovery probability (*f*), ± SE and 95% CL's for Ross's geese marked at MCR and QMG, 2003–2005.

Origin and marker type	Parameter	Estimate	SE	LCL	UCL
MCR legband	*S*	0.7743	0.0555	0.6479	0.8647
QMG legband	*S*	0.7744	0.0555	0.6482	0.8648
MCR reward-legband	*S*	0.7818	0.0573	0.6497	0.8738
QMG reward-legband	*S*	0.7816	0.0572	0.6497	0.8735
MCR colour neckband	*S*	0.5300	0.0362	0.4589	0.5998
QMG colour neckband	*S*	0.5298	0.0362	0.4587	0.5997
MCR white neckband	*S*	0.5306	0.0370	0.4579	0.6020
QMG white neckband	*S*	0.5303	0.0370	0.4575	0.6017
MCR legband	*f*	0.0236	0.0023	0.0195	0.0285
QMG legband	*f*	0.0171	0.0016	0.0143	0.0205
MCR reward-legband	*f*	0.0304	0.0031	0.0250	0.0370
QMG reward-legband	*f*	0.0242	0.0027	0.0195	0.0301
MCR colour neckband	*f*	0.0423	0.0029	0.0370	0.0483
QMG colour neckband	*f*	0.0355	0.0026	0.0308	0.0410
MCR white neckband	*f*	0.0403	0.0031	0.0346	0.0468
QMG white neckband	*f*	0.0348	0.0027	0.0298	0.0406

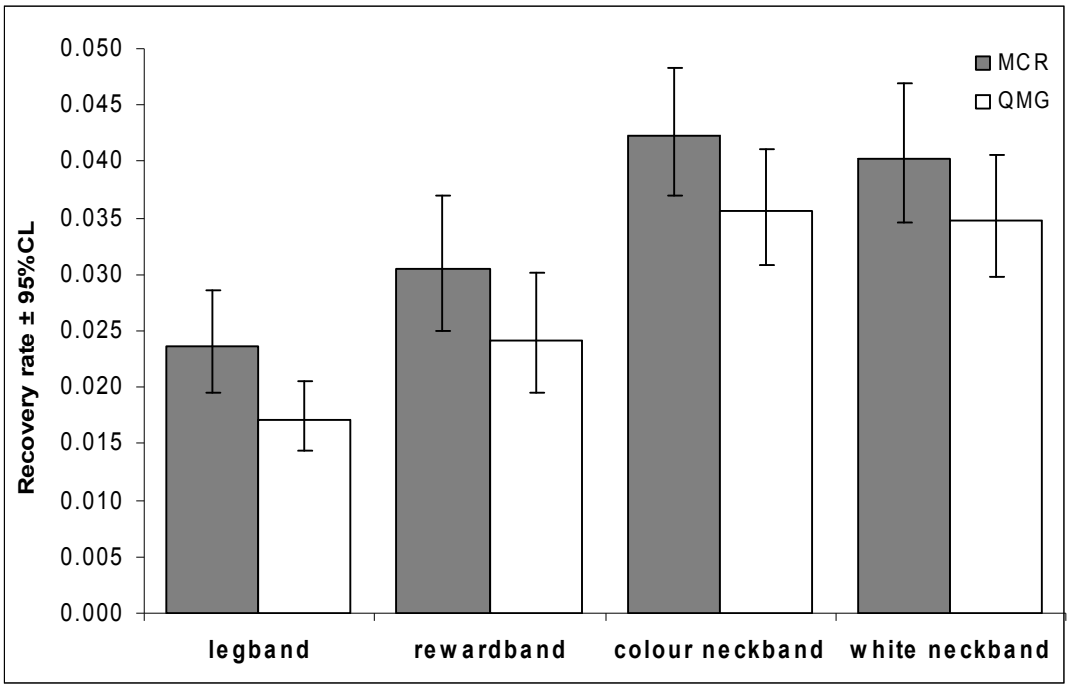

Figure A.2. Recovery rate estimates (± 95% CL) of Ross's geese marked at MCR and QMG by nesting colony and marker type (2003–2005).

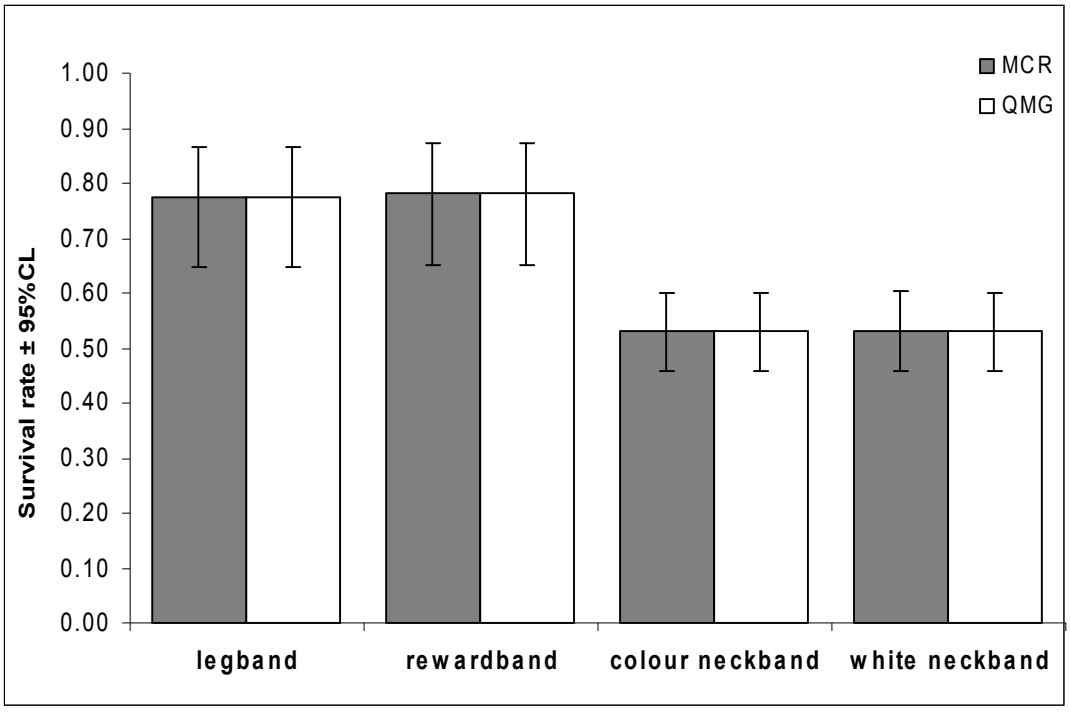

Figure A.3. Survival rate estimates (± 95% CL) of Ross's geese marked at MCR and QMG by nesting colony and marker type (2003–2005).